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ENVIRONMENTAL FACTORS REGULATING THE BIOMASS AND DIVERSITY OF AQUATIC MACROPHYTE COMMUNITIES IN RIVERS

BY

TODD DOUGLAS FRENCH ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements of the degree of MASTER OF SCIENCE.

DEPARTMENT OF BIOLOGICAL SCIENCES

Edmonton, Alberta

FALL 1995

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled ENVIRONMENTAL FACTORS REGULATING THE BIOMASS AND DIVERSITY OF AQUATIC MACROPHYTE COMMUNITIES IN RIVERS here submitted by TODD DOUGLAS FRENCH in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

Dr. P. A. Chambers, Environment Canada

Dr. E. E. Prepas, Biological Sciences

Dr. D. H. Vitt, Biological Sciences

Dr. N. Rajaratnam, Civil Engineering

June 29 1995

ABSTRACT

Aquatic macrophytes in the Nechako River, British Columbia, Canada, currently cover up to 46% of the river bottom and have biomasses up to 1262 $g \cdot m^{-2}$ dry weight. While no information is available on submerged macrophyte abundance prior to regulation in 1952, future reductions in summer discharge from current conditions of 164 $m^3 \cdot s^{-1}$ (June 15 - August 15; 1952 - 1990) in the Upper Nechako River could increase submerged macrophyte abundance. To quantify the relationship between environmental factors and macrophyte abundance in the Nechako River depth, current speed, sediment grain size, and sediment exchangeable nitrogen (N) and phosphorus (P) concentrations were measured at 5-m intervals along 26 cross-stream transects spanning a river distance of 203 km. Macrophyte abundance was positively correlated with sediment exchangeable N (r = 0.51; $P < 0.0001$) and P (r = 0.61; $P < 0.0001$) concentrations and negatively correlated with current speed (r = -0.80; $P < 0.0001$), depth (r = -0.30; P = 0.01) and sediment grain size (r = -0.68; $P < 0.0001$). Empirical models relating bottom cover (r^2 = 0.80) and cross-sectional biomass (r^2 = 0.82) to mean summer channel speed were used to predict macrophyte abundance prior to initial discharge regulation in 1952 and for future discharge-reduction scenarios. The models predict that bottom cover and cross-sectional biomass could increase up to 3- and 12-fold, respectively, in certain reaches of the river.

To test the hypothesis that riverine macrophyte abundance and community structure are functions of river basin morphometry, macrophyte distribution was related to both small scale (near shore cross-sectional slope) and large scale (catchment area and longitudinal slope) aspects of basin morphometry for the Nechako River. Macrophyte bottom cover was found to vary with the longitudinal slope of the river such that two high (0.5 $m \cdot km^{-1}$) gradient reaches had low (2.4 ± 1.3% and 5.6 ± 3.4%; mean ± 1 S.E.) macrophyte bottom cover, whereas a lower (0.2 $m \cdot km^{-1}$) gradient reach had significantly ($P < 0.0001$) greater cover (28.1 ±

3.4%). Tracheophyte diversity (gamma diversity, H') increased along the length of the river such that H' was 2.1, 1.7 and 0.5 in reaches of high (42500 km^2), moderate (25100 km^2) and low (23730 km^2) catchment area, respectively. In view of the river continuum and intermediate disturbance hypotheses, it is possible that the observed downstream increase in macrophyte diversity is attributable to the greater temporal variability in discharge in the downstream reaches; where discharge variability is a function of catchment area. Taxonomic dominance also varied along the river with *Potamogeton pectinatus*, mosses and *Potamogeton berchtoldii* dominating the downstream reach with high catchment area, and *Elodea canadensis*, *Potamogeton richardsonii*, *Myriophyllum exalbescens* and *Ranunculus aquatilis* dominating reaches of moderate and low catchment area. On a small scale, peak biomass was inversely correlated ($P < 0.001$) with near shore cross-sectional slope, an observation consistent with similar findings for the Bow River, Alberta, and Lake Memphremagog, Quebec/Vermont.

Analyses of macrophyte species abundance in relation to physical characteristics of the littoral zone showed that gradients of current speed, sediment texture and depth determined the relative abundance of macrophyte taxa such that macrophyte species inhabited different microenvironments within the river's littoral zone. Some taxa were highly specific to certain environmental conditions. Thus, *Ceratophyllum demersum* occurred almost exclusively at sites with current speeds < 0.2 $m \cdot s^{-1}$, moderate depths (1.5 - 2.0 m) and silty substrates (14 - 56 μm). In comparison, mosses were most prevalent at sites with current speeds > 0.6 $m \cdot s^{-1}$, depths < 1.5 m and substrates of bare rock. *Callitriche hermaphroditica* and *Potamogeton gramineus*, while not as specific as mosses and *C. demer*sum with respect to current speeds and substrate, were almost always found at depths < 1.5 m. A reciprocal transplant experiment in which *E. canadensis* were grown within and outside monospecific stands of *E. canadensis* on sediments collected from within or outside the stand showed that the presence of *E. canadensis* can facilitate the growth of conspecifics, irrespective of sediment type. Thus, *E. canadensis*

attained an average biomass of 16.1 ± 3.1 g when grown in the presence of conspecifics, while very little (0.2 ± 0.1 g) growth occurred when grown in the absence of conspecifics.

In summary, this study showed that the distribution of macrophytes in rivers is controlled by current speed, sediment texture, sediment nitrogen and phosphorus concentrations, and depth. It was also shown that the structure of riverine macrophyte communities is a function of both small scale (near shore cross-sectional slope) and large scale (catchment area and longitudinal slope) morphometry. The finding that macrophyte taxa are segregated by physical gradients in rivers is consistent with current evolutionary theory which holds that selection pressure drives species within a community to partition essential resources so as to minimize competition. The results of this study are particularly relevant when considering the effects of river impoundment activities on riverine macrophyte communities in that decreases in channel speed and temporal discharge variability resulting from impoundment may result in increased macrophyte abundance and decreased species diversity, respectively.

Acknowledgements

The surveys and experiments undertaken in this study were conducted *in situ* and were largely performed underwater with the use of SCUBA. Thus, I am grateful for the hard work of Ms. Natasha King and Mr. Warren Zyla who assisted me in the field over the 1992 and 1993 field seasons, respectively. I also thank Ms. Trinh Luong (Environment Canada) and Mr. Darren Schill (Environment Canada) for performing sediment nutrient and grain size analyses, respectively; Dr. Michael Agbeti (University of Alberta), Dr. Dale Vitt (University of Alberta), Dr. Ellie Prepas (University of Alberta), Mr. Bill Aitken (Environment Canada) and Dr. Barney Kenney (Environment Canada) for valuable discussion; the College of New Caledonia (Prince George, B. C.) for providing lab space for the 1992 and 1993 summers; and the Meanook Biological Research Station (Athabasca, Alberta) for providing boats, motors and other equipment. Dr. Carlos Duarte (Centro de Estudios Avanzados de Blanes, Girona, Spain) provided macrophyte and littoral slope data for Lake Memphremagog which was used in my study of morphometric determinants of macrophyte abundance and distribution (Chapter 3).

This project was inspired by Mr. Bruce Carmichael (British Columbia Ministry of Environment, Prince George, B. C.) and Mr. Colin McKean (British Columbia Ministry of Environment, Victoria, B. C.) who were interested in the possible effects of river impoundment on aquatic macrophyte communities. Their premise that flow reductions in rivers might result in changes in riverine macrophyte communities formed the basis for my masters thesis and I am grateful that they shared their ideas with me.

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Part I. Background to study

1. General Introduction

While dams have been built for the purpose of river regulation for over 5000 years, most existing dams were built in the 1900's (Smith 1971). On a world-wide scale, more than 12000 dams > 15 m in height were constructed by 1971, with over 8000 of these being built between 1945 and 1971 (Beaumont 1978; Petts 1984). Today, Petts (1984) reports that most of the world's major rivers are impounded to some degree.

With the extent of dam-building activities world-wide, much scientific information has been gathered in regards to physical changes in rivers resulting from impoundment. For example Dickson (1975) and Hall *et al.* (1977) have reported substantial decreases in annual runoff for the Churchill River, Canada, and the Zambezi River, Mozambique, since their impoundment, respectively. Gordon *et al.* (1992) and King and Tyler (1982) also indicate that impoundment can decrease seasonal discharge variability while Elliot and Engstrom (1959), Dolan *et al.* (1974) and Guy (1981) have shown that impoundment can change the periodicity of annual extremes. In addition, dams have been shown to alter the chemistry, sediment transport capability, temperature and nutrient cycles of rivers (Gordon *et al.* 1992). For example, the hypolimnetic release waters from some dams may be anoxic and contain reduced compounds which may increase the oxygen demand of release waters and be toxic to aquatic organisms (Ward 1982). Gordon *et al.* (1992) reported that discharge reduction and elimination of peak flows often results in the accumulation of fine sediments in the streambed gravels of regulated rivers, reducing the river's suitability for spawning and causing changes in the structure of benthic invertebrate communities. Because the channel velocity of a river is positively correlated with discharge (Gordon *et al.* 1992), reductions in discharge resulting from impoundment can also affect the velocity

regime of a river.

Given that riverine biota must be adapted to the physical and chemical regimes of lotic environments in order to exist, changes in these regimes brought about by impoundment should be expected to have ecological effects. Thus, Bain *et al.* (1988) found differences in fish species composition and abundance in a comparison of regulated and unregulated rivers. Similarly, Fenner *et al.* (1985) found that the reduction in floodplain area resulting from river impoundment decreased the frequency with which floodplain vegetation was inundated, resulting in changes in floodplain plant communities. Gordon *et al.* (1992) also reported that changes in the sediment transport and temperature regimes following impoundment can change benthic invertebrate and aquatic insect community structure, respectively.

In northern British Columbia, Canada, a major hydroelectric development is currently under review which, if permitted, would divert much of the remaining flow of the Nechako River, a major tributary of the Fraser River, to a different watershed. Analyses of historical discharge data for the Nechako River have shown that the initial impoundment of the Nechako River in 1952 has severely reduced both annual discharge in the river and seasonal discharge variability (French and Chambers 1993). An aerial survey of the Nechako River performed in September 1991 showed that aquatic plants (macrophytes) were concentrated in the middle reaches of the river and often occupied more that 30% of the channel (French and Chambers 1993) (Fig. 1). While no information is available on the abundance of macrophytes prior to the river's impoundment, anecdotal information suggests that the large growths of macrophytes currently present in the middle reaches of the Nechako River developed following impoundment. In support of this, numerous studies have documented changes in macrophyte communities following impoundment. For example, Holmes and Whitton (1977) observed

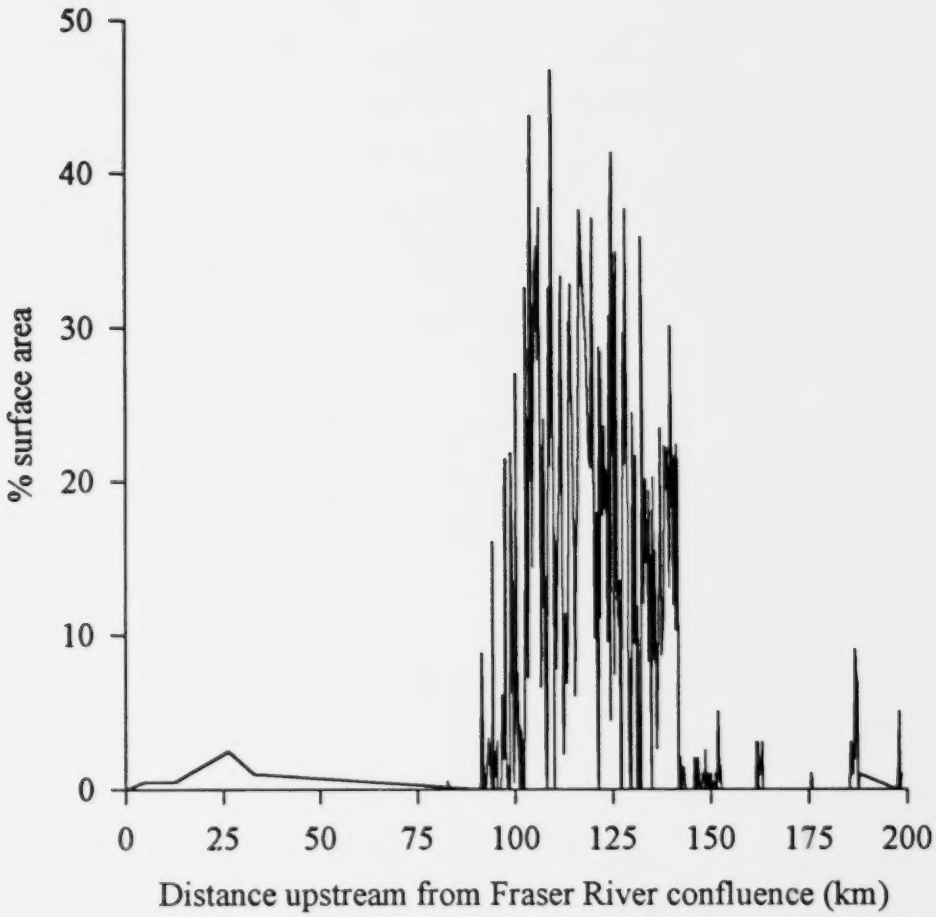

FIGURE 1. Surface area (%) of the Nechako River, British Columbia, covered by submerged aquatic macrophytes as determined by an aerial survey conducted in September 1991 (from French and Chambers 1993).

substantial increases in *Potamogeton crispus*, *Zannichellia palustris* and *Myriophyllum spicatum* in the Tees River, England, following impoundment. Similarly, Rorslett et al. (1989) reported that macrophyte abundance increased dramatically in the Otra, Suldalslagen and Borsleva rivers, Norway, following impoundment.

The objective of the research presented herein was to quantify the environmental factors regulating the biomass, distribution and species composition of lotic macrophyte communities and to use this basic information as a framework to predict changes in macrophyte community structure resulting from reduced-flow conditions. To address this objective, three projects were undertaken.

Project 1 (Chapter 2): Predicting Changes in Macrophyte Abundance under Altered Discharge Regimes

The purpose of this project was to quantify the relationship between environmental conditions (i.e., instantaneous current speed, bottom sediment nutrient availability, bottom sediment grain size and depth) and submerged macrophyte abundance in lotic systems and to develop an empirical model based on mean channel speed to predict changes in macrophyte abundance following the second stage of impoundment of the Nechako River.

Project 2 (Chapter 3): Relationship between Basin Morphometry and the Diversity and Abundance of Riverine Macrophytes

The aim of this study was to test the hypothesis that macrophyte abundance (biomass and bottom cover) and community structure (species composition and diversity) are functions of both small scale (near shore cross-sectional slope) and large scale (catchment area and longitudinal slope) characteristics of river basin morphometry. This study discusses the implications of decreases in discharge

variability in terms of the river continuum concept (e.g., Vannote *et al.* 1980) and the intermediate disturbance hypothesis (e.g., Connell 1978; Ward and Stanford 1983).

Project 3 (Chapter 4): Niche Partitioning of Macrophytes in Lotic Systems

The purpose of this study was to investigate how environmental resources are partitioned amongst riverine taxa with empirical data and to test the hypothesis that the presence of macrophytes can facilitate the growth of other macrophytes using an *in situ* experimental approach. The results of this study are relevant to species-specific impacts of river diversions.

References Cited

BAIN, M. B., J. T. FINN, AND H. E. BOOK. 1988. Streamflow regulation and fish community structure. Ecology **69:** 382-392.

BEAUMONT, P. 1978. Man's impact on river systems: a world-wide view. Area **10:** 38-41.

CONNELL, J. H. 1978. Diversity in tropical rainforests and coral reefs. Science **199:** 1302-1310.

DICKSON, L. W. 1975. Hydroelectric development of the Nelson River system in northern Manitoba. J. Fish. Res. Board Can. **32:** 10-16.

DOLAN, R., A. HOWARD, AND A. GALLENSON. 1974. Man's impact on the Colorado River in the Grand Canyon. Am. Sci. **62:** 392-401.

ELLIOT, R. A., AND L. R. ENGSTROM. 1959. Controlling floods on the Tennessee. Civ. Eng. **29:** 60-63.

FENNER, P., W. B. WARD, AND D. R. PATTON. 1985. Effects of regulated water flows

flows on regeneration of Fremont cottonwood. J. Range Manage. **38:** 135-138.

FRENCH, T. D., AND P. A. CHAMBERS. 1993. Aquatic macrophytes in the Nechako River, British Columbia: Part II. Environmental factors regulating the growth of aquatic macrophytes. National Hydrology Research Institute, Environment Canada, Saskatoon, Saskatchewan, NHRI Contribution No. CS-93993.

GORDON, N. D., T. A. MCMAHON, AND B. L. FINLAYSON. 1992. Stream hydrology, an introduction for ecologists. John Wiley & Sons, Toronto. 526 pp.

GUY, P. R. 1981. River bank erosion in the mid-Zambezi Valley, downstream of Lake Kariba. Biol. Conserv. **20:** 199-212.

HALL, A. E., I. VALENTE, AND B. R. DAVIES. 1977. The Zambezi River in Mozambique: the physico-chemical status of the Middle and Lower Zambezi prior to the closure of the Cabora Bassa Dam. Freshwater Biol. **7:** 187-206.

HOLMES, N. N. H., AND B. A. WHITTON. 1977. The macrophytic vegetation of the River Tees in 1975: observed and predicted changes. Freshwater Biol. **7:** 43-60.

KING, R. D. AND P. A. TYLER. 1982. Downstream effects of the Gordon River Power Development, south-west Tasmania. Aust. J. Mar. Freshwater Res. **33:** 431-442.

PETTS, G. E. 1984. Impounded rivers, perspectives for ecological management. John Wiley and Sons, Toronto. 326 pp.

RORSLETT, B., M. MJELDE, AND S. W. JOHANSEN. 1989. Effects of hydropower development on aquatic macrophytes in Norwegian rivers: present state of knowledge and some case studies. Regul. Rivers Res. & Manage **3:** 19-28.

SMITH, N. 1971. A history of dams. Peter Davies, London. 279 pp.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37:** 130-137.

WARD, J. V. 1982. Ecological aspects of stream regulation: responses in downstream lotic reaches. Wat. Poll. Manage. Rev. **2:** 1-26.

WARD, J. V., AND J. A. STANFORD. 1983. The intermediate-disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. Pages 347-356 *in* T. D. FONTAINE AND S. M. BARTELL [Eds.]. Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, Michigan.

Part II. Abiotic factors controlling aquatic macrophyte community structure in flowing water

2. Aquatic macrophyte community structure in flowing water in relation to current velocity, sediment properties and depth with emphasis on the potential effects of river impoundment[1]

Introduction

In terrestrial systems, the distribution of plants along environmental gradients such as latitude, altitude, topography, aspect, temperature, nutrients and proximity to water, have been well studied and quantified (Barbour *et al.* 1987). In contrast, very little research has investigated the relationship between the distribution of submerged aquatic plants (macrophytes), particularly riverine macrophytes, and environmental conditions (Haslam 1987). This may be due to the fact that terrestrial plants are more directly linked to societal requirements (food) and the economy (agriculture and forestry) than are macrophytes. Detailed work may also be lacking in rivers because of the practical difficulties associated with working in flowing water and, by comparison to lakes, because rivers tend to be less diverse with respect to macrophyte species (Bilby 1977). Macrophytes, however, grow abundantly in many of the world's rivers (Haslam 1978). They are important components of aquatic ecosystems in that they are primary producers (Pokorny *et al.* 1984), provide a living substrate for epiphytic algae (Cattaneo and Kalff 1980) and provide shelter (Whitehead 1935; Harrod 1964), oviposition sites (McGaha 1952) and food for aquatic invertebrates (Pip and Stewart 1976; Sheldon 1987; Chambers *et al.* 1990). However, excessive macrophyte abundance may have detrimental effects, including impeding boat and float-plane traffic and recreational activities (Rorslett *et al.* 1989; Chambers *et al.* 1991), altering streamflow patterns and increasing the potential for flooding (Gregg and Rose

[1]A version of this chapter will be submitted for publication in *Canadian Journal of Fisheries and Aquatic Sciences.*

1982; Madsen and Warncke 1983), affecting water chemistry (e.g., Buscemi 1958; Chittenden *et al.* 1976; Mayes *et al.* 1977; Rawlence and Whitton 1977; Rorslett *et al.* 1985) and causing temporal (diurnal and seasonal) fluctuations in dissolved oxygen concentration, due to the combined effects of respiration and decomposition which, in turn, can cause fish mortality (e.g., Butcher 1933; Brooker *et al.* 1977). Yet despite the importance of macrophytes in riverine systems, little is known of the environmental factors regulating their abundance and distribution.

The aim of this study was to evaluate the environmental factors regulating macrophyte abundance in a lotic system prior to further impoundment. Few studies have investigated the impact of impoundment on riverine macrophyte communities however amongst those which have, large-scale river impoundments have generally been associated with increased development of macrophyte communities. For example, Petts (1984) reported massive increases in macrophyte abundance following the impoundment of the Sutlej River, India, the Volta River, Ghana, the Zambezi River, Rhodesia, and the Tuolumne River, California. Similarly, Rorslett (1988) reported substantial increases in macrophyte abundance following the impoundment of the Otra River, Norway. Increases in aquatic macrophyte abundance following impoundment can, in turn, affected higher trophic levels. Impairment and, in some cases, total blockage of salmonid migration has been attributed to increased macrophyte growth in the Tuolumne River following impoundment (Fraser 1972), while detrimental changes to hippopotamus, crocodile and wildfowl populations have been reported in the Zambezi River (Attwell 1970). Yet despite the potential for changes in riverine macrophyte communities following river impoundment, there have been few, if any, studies which attempt to predict changes in macrophyte communities prior to dam construction so that macrophyte management strategies could be implemented before excessive macrophyte growth occurs. This paper presents the results of an *in situ* study to: (1) quantify the relationship between environmental conditions and submerged macrophyte

abundance in a lotic system, and (2) predict changes in macrophyte abundance following the second stage of impoundment of the Nechako River (north central British Columbia, Canada). The results of this study are particularly pertinent given the importance of macrophytes in lotic ecosystems and the extent of dam-building activities world-wide (Petts, 1984).

Methods and Materials

Study site

The Nechako River, located in central British Columbia, is one of the largest tributaries of the Fraser River, having an average annual discharge of 9180000 dam^3 (Environment Canada 1991). Prior to the construction of the Kenney Dam (*circa* 1952), the Nechako River arose from Knewstubb Lake and flowed northward for 8 km via the Nechako Canyon to where it joined the Cheslatta River (Fig. 1). However, since 1952 essentially all discharge into the Nechako Canyon has been blocked by the Kenney Dam, with the water being diverted into a 906 km^2 reservoir located upstream of the Nechako Canyon. Water required for power generation is removed from the west end of the reservoir, diverted through a tunnel to the coast and falls 792 m to the Pacific Ocean. Thus, completion of the Kenney Dam resulted in much of the Nechako's water being diverted into a different watershed. Water not needed for power generation is released into the Cheslatta River; thus the outflow of Cheslatta Lake is now the beginning of the Nechako River.

The present Nechako River flows northeast from the Cheslatta River for 83 km to the village of Fort Fraser (population ~ 500) (Fig. 1) and then northwest for 4.5 km to where it converges with the Nautley River which drains Fraser and Francois lakes. The Nechako then flows southeast for 196 km to where it joins

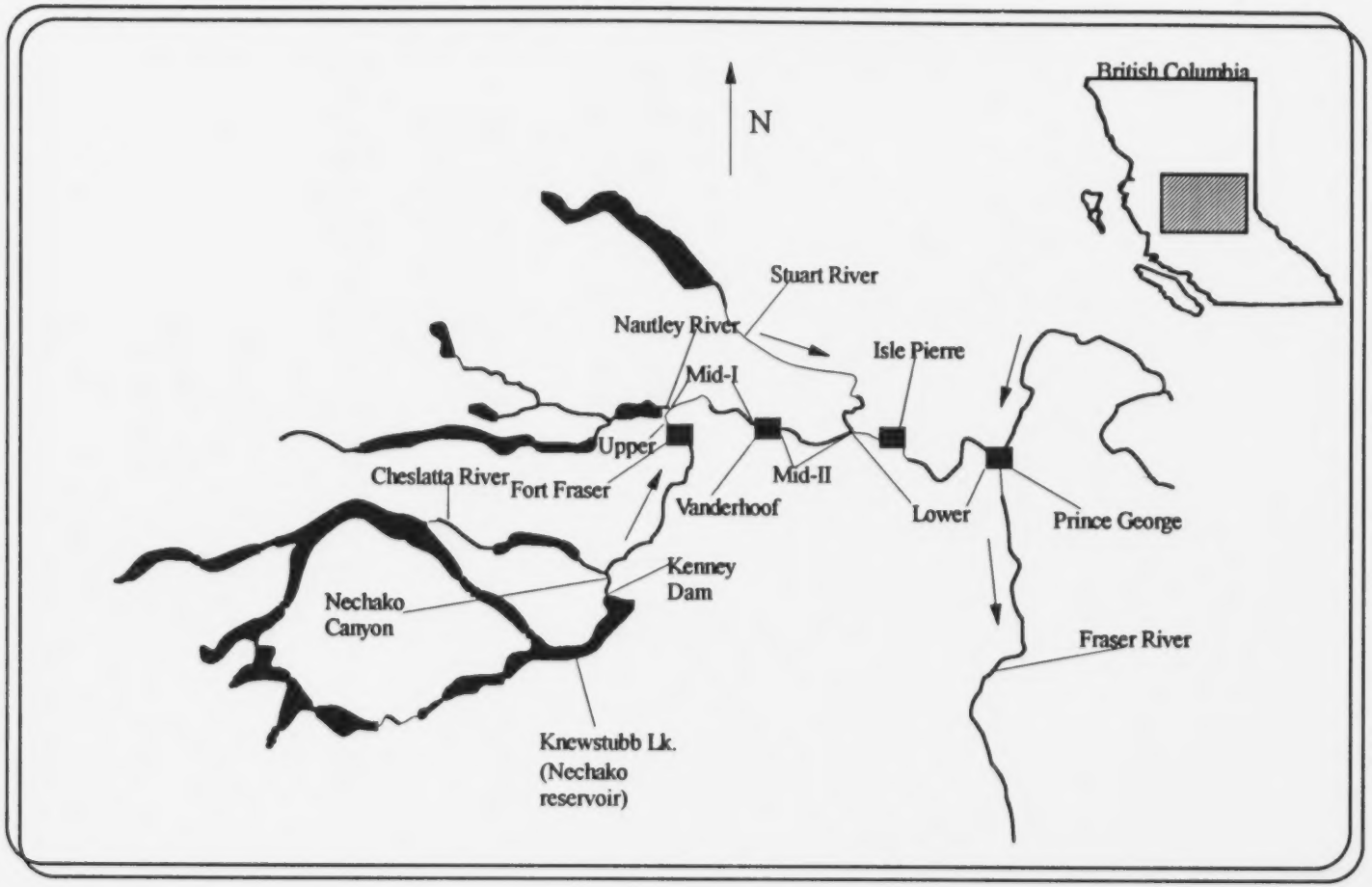

FIGURE 1. Map of the Nechako River, British Columbia, showing location of Upper, Mid-I, Mid-II and Lower reaches.

with the Fraser River at the city of Prince George (population ~ 71000). Between its confluence with the Nautley River and Prince George, the Nechako River flows through the town of Vanderhoof (population ~ 4000) and is joined by its largest tributary, the Stuart River. Throughout its length, the Nechako River is well entrenched and, thus, only overflows its banks during extraordinary high-flow events.

In 1992, 26 sites were selected over a 203 km distance from 7 km upstream of the Nautley River to the confluence with the Fraser River. The river was divided into four reaches based on physical characteristics: (1) Upper Nechako (upstream of the Nautley River) characterized by slow channel speed and shallow depths; (2) Mid-I (Nautley River to Vanderhoof) characterized by fast channel speed and shallow depths; (3) Mid-II (Vanderhoof to Stuart River) characterized by slow channel speed and shallow depths; and (4) Lower Nechako (downstream of the Stuart River) characterized by fast channel speed and deep depths. Sites were selected from each of the four regions from 1:50000 maps (British Columbia Department of Energy, Mines and Resources 1977) to encompass a wide range in water depth and current speed.

Hydrology

(a) Discharge

Long-term daily discharge data were obtained from Environment Canada (1991) for three water survey stations on the Nechako River: (1) Fort Fraser in the Upper Nechako (54° 03' 18" N, 124° 33' 39" W); (2) Vanderhoof at the juncture of Mid-I and Mid-II reaches (54° 01' 34" N, 124° 14' 01" W); and (3) Isle Pierre in the Lower Nechako (53° 57' 37" N, 123° 14' 01" W). Long-term daily discharge data were also obtained for the Nechako River's two largest tributaries: (1) Nautley River (54° 05' 07" N, 124° 35' 58" W) and (2) Stuart River (54° 25' 05" N, 124° 16' 30" W). All stations had data for the period since the completion of the

Kenney Dam (post-KDC; 1952-1990). Thus, post-KDC discharge data for the Upper, Mid-I and Mid-II and Lower Nechako are from the Fort Fraser, Vanderhoof and Isle Pierre stations, respectively. Data prior to the completion of the Kenney Dam (pre-KDC) were available only for the Vanderhoof (1915 and 1948-1951) and Stuart River (1929-1952) stations. Thus, pre-KDC discharge of the Upper Nechako was estimated as the difference between the discharge at Vanderhoof pre-KDC and the discharge of the Nautley River post-KDC (this assumes that inputs from the catchment is negligible between Fort Fraser and the Nautley River and that the average discharge of the Nautley River has not been affected by the Kenney Dam). Pre-KDC discharge of the Lower Nechako was estimated as the sum of the discharge at Vanderhoof pre-KDC and the discharge of the Stuart River pre-KDC (this assumes that input from the catchment is negligible between Vanderhoof and the Stuart River). Pre-KDC discharge for both the Mid-I and Mid-II reaches was assigned the pre-KDC values for Vanderhoof.

Comparisons of pre- and post- KDC data showed that the Kenney Dam has decreased the seasonal variability in discharge in the Upper, Middle and Lower Nechako (Fig. 2). The effect of the Kenney Dam is less in the Lower Nechako due to the buffering effects of tributaries and other catchment inputs to the Nechako mainstem. Prior to the construction of the Kenney Dam, summer (June 15 - August 15) discharge averaged ~ 408, ~ 468 and ~ 699 $m^3 \cdot s^{-1}$ for the Upper, Middle and Lower Nechako, respectively. However, since the completion of the Kenney Dam the average summer discharge for the Upper, Middle and Lower Nechako has decreased to ~165, ~ 224 and ~ 525 $m^3 \cdot s^{-1}$, respectively. Further impoundment proposed for the Nechako River may reduce average summer discharge in the Upper Nechako River at Fort Fraser to ~ 120 or ~ 60 $m^3 \cdot s^{-1}$ (Table 1).

(b) Channel speed

To estimate the mean channel speed (the average velocity of the channel at

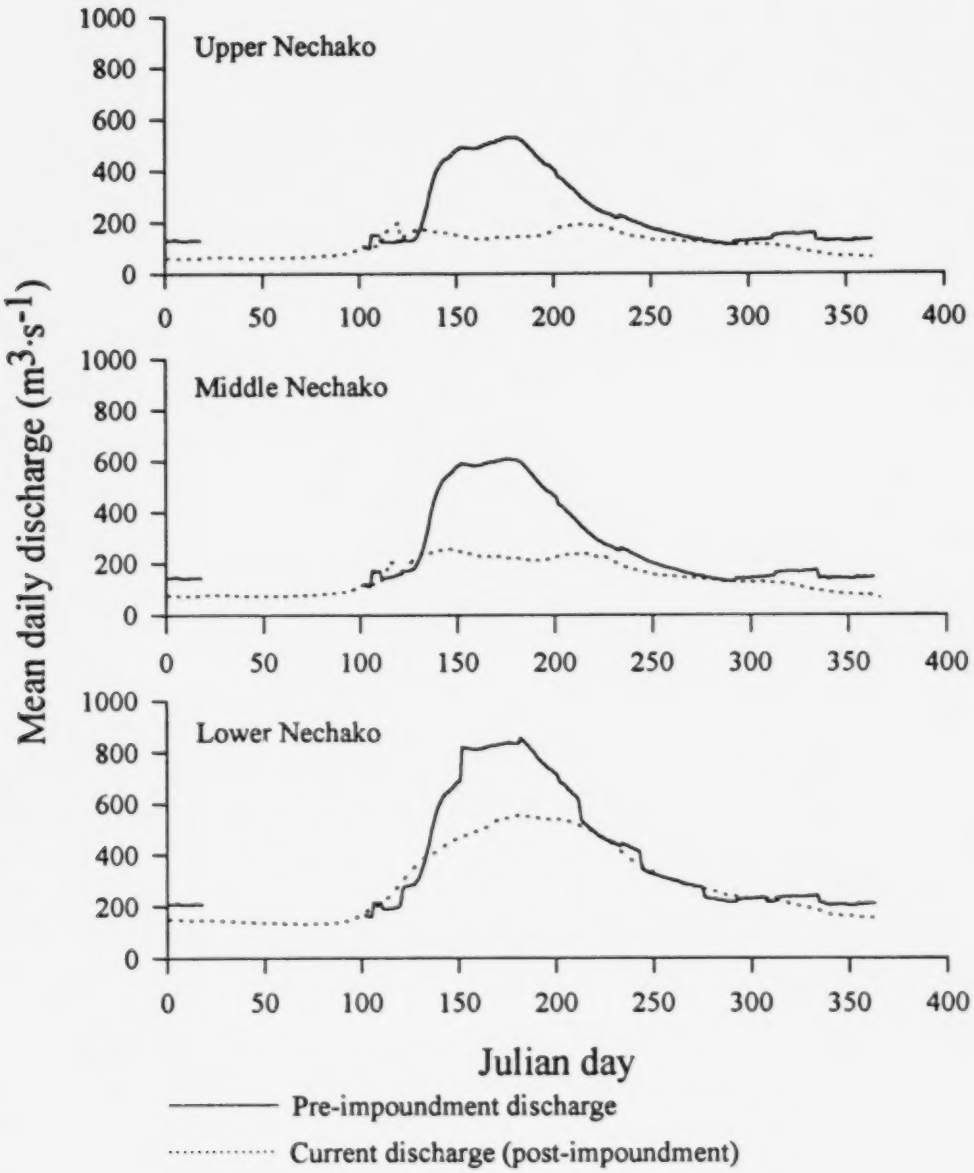

FIGURE 2. Hydrologic cycle of the Upper, Middle and Lower Nechako River, British Columbia.

TABLE 1. Mean summer (June 15 - August 15) discharge ($m^3 \cdot s^{-1}$) for the Upper, Middle and Lower Nechako River, British Columbia, the year the survey was conducted (1992), prior to the construction of the Kenney Dam (prior to 1952) and for two discharge regimes which represent possible scenarios following the second stage of impoundment. (Data for 1952-1990 and 1992 for all stations and for pre-1952 for the Upper Nechako from Environment Canada. All other data estimated following methods in text).

Discharge Regime	Upper @ Fort Fraser ($m^3 \cdot s^{-1}$)	Mid @ Vanderhoof ($m^3 \cdot s^{-1}$)	Lower @ Isle Pierre ($m^3 \cdot s^{-1}$)
Pre-1952	407	467	698
Mean 1952-1990	165	224	525
1992	194	230	516
Regime I	120	180	434
Regime II	60	117	371

a given cross-section) for each site, data relating river width, discharge and cross-sectional area were obtained from Environment Canada (Water Resources Branch, Vancouver, British Columbia) for the three water survey sites on the Nechako River for each date the survey station was calibrated. Mean channel speed was calculated for each calibration date by:

$$V = \frac{Q}{A} \quad \textit{(Gordon et al.} \text{ 1992)} \quad (1)$$

where V is mean channel speed ($m \cdot s^{-1}$), Q is discharge ($m^3 \cdot s^{-1}$) and A is cross-sectional area (m^2). Using non-linear regression (Norusis 1993), a curve (hereinafter referred to as the "standard curve") was fit to the channel speed vs. discharge data for each station (Fig. 3). The curve for the Fort Fraser water survey station was then applied to sites in the Upper Nechako while the curves for the Vanderhoof and Isle Pierre water survey stations were applied to sites in the Middle and Lower Nechako, respectively. Assuming that discharge is approximately constant within each of the three hydrologic sections (i.e., Upper, Middle and Lower Nechako), the velocity vs. discharge relationship will vary between sites within a given hydrologic section due to differences in cross-sectional area. To calibrate the channel speed vs. discharge curve to each site, the y-intercept of the standard curve was shifted vertically (up or down) so that the curve passed through a known coordinate (i.e., a point of known channel speed and discharge) for each of the 26 sites. The known coordinate for each site was determined by measuring the cross-sectional area for each site on a given date, estimating discharge for that date (as described in "discharge" section) and calculating channel speed from equation 1. The mean summer (June 15 - August 15) channel speed was then estimated by determining the mean summer discharge for each of the study sites and interpolating the associated current speed from the channel speed vs. discharge

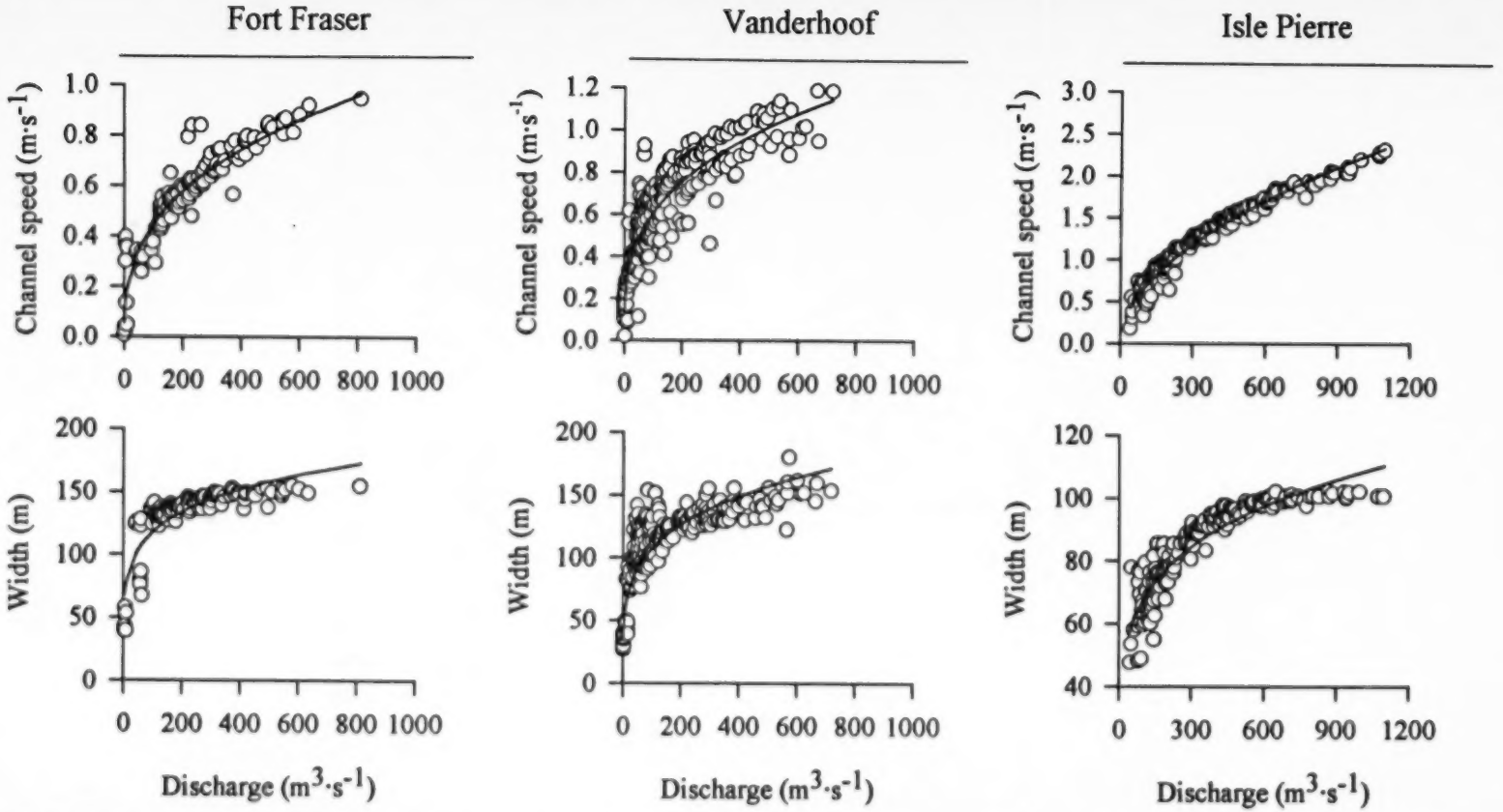

FIGURE 3. Relationships between channel speed ($m \cdot s^{-1}$) and width (m) versus discharge ($m^3 \cdot s^{-1}$) for the Nechako River, British Columbia, at Fort Fraser, Vanderhoof, and Isle Pierre (data from Environment Canada, Water Resources Branch, Vancouver, British Columbia).

curve.

Field sampling methods

In August 1992, submerged macrophytes (excluding below-ground structures) were harvested using SCUBA (Self Contained Underwater Breathing Apparatus) from within three 0.1 m^2 quadrats placed at 5-m intervals across the channel at each site. Collections proceeded towards centre-stream from each bank to 10 m beyond the maximum depth of colonization. Two sediment cores (4 cm diameter; ~ 10 cm length) were also collected from within each quadrat. The cores were extruded on site and the top 5 cm frozen until analysis. Depth was measured at each sampling interval with a weighted-rope marked at 0.1-m intervals. Current speed (current speed measured at a particular point in the river is referred to as "localized current speed" or "instantaneous current speed" in text) was measured at each sampling interval with a Price AA current meter following the procedure of Gray (1973). For depths > 1.5 m, current speed was measured at three depths: (1) surface (0.8 × total depth), (2) mid-depth (0.5 × total depth) and (3) bottom (0.2 × total depth). For depths < 1.5 m, current speed was measured only at mid-depth. Average current speed was calculated for sites > 1.5 m as the mean of three readings taken at the surface, mid-depth and bottom. Current speed was not measured when plants impeded the meter's bucket wheel. In summer 1993, cross-sectional area of the riverbed was determined for each site. At each site a rope marked at 1-m intervals was suspended across the river and depth was measured at 1- or 5-m intervals for small or large changes in depth, respectively, with a rigid pole marked at 0.1-m increments or, in deep (> 3 m), fast (> 0.5 $m \cdot s^{-1}$) conditions, with a depth sounder.

Laboratory analyses

Macrophyte samples were cleaned with tap water to remove invertebrates

and debris, sorted to species with keys in Warrington (1980), dried at 80°C to constant weight and weighed to 0.01 g with a Mettler College Deltarange balance (model 2440). Macrophyte biomass was calculated as a mean of the three replicates from each interval and expressed as plant mass ($g \cdot m^{-2}$ dry weight). Exchangeable nitrogen (N) and phosphorus (P) concentrations were determined from frozen sediment samples after they were thawed to room temperature. Duplicate samples from within each quadrat were pooled prior to analysis; all analyses were performed in duplicate. Exchangeable P was extracted from 0.25 g of homogenized wet sediment by shaking (16 h) in 25 ml of 0.1 N NaOH + 0.1 N NaCl (after Williams *et al.* 1967) and measured spectrophotometrically (Murphy and Riley 1962). Exchangeable N was extracted from 4 g of homogenized wet sediment by shaking (1h) in 40 ml of 2 M KCl (Bremner 1965) and measured spectrophotometrically as ammonium (Solorzano 1969). Particle size distribution (expressed as phi) was determined in triplicate with a Malvern 2600L laser particle size analyzer (LPSA) for 100 samples selected to encompass sites covering the full range in current speeds. Sediment samples were put into the waterbath of the LPSA after wet-sieving through a 1.5 mm sieve. Disaggregation of sediment samples was achieved by both mechanical stirring and ultrasonic dispersion in the waterbath. Three distributions were measured on each sample and the results averaged. Particle size was measured on the phi (Φ) scale (the negative logarithm in base 2 of the particle size in mm) (Gordon *et al.* 1992) and converted to micrometers by the equation:

$$\mu m = antilog(-\phi \cdot \log_{10}2) \cdot 1000 \quad (2)$$

Macrophyte and sediment samples were processed within 1 year of collection.

Measures of community structure

To investigate the relationship between mean summer channel speed and macrophyte community structure, species richness (the total number of species present) and species diversity were calculated for each survey transect (alpha diversity; Whittaker 1972; Vitt *et al.* 1995) and related to mean summer channel speed. Alpha diversity was calculated as:

$$H' = \sum_{i-1}^{s} p_i(\log_2 p_i) \quad (3)$$

where H' is the Shannon-Wiener index of diversity (Krebs 1989), s is the number of species observed in the transect and p_i is the proportion of the total biomass belonging to the *ith* species. Because mosses and macroscopic algae (i.e., *Chara*) were not identified to species, they were not included in diversity or richness computations. Taxonomic dominance was also related to instantaneous current speed.

Statistical analyses

Data were analyzed with the statistical computer program SPSS version 6.0 (Norusis 1993) following the procedures outlined in Norusis (1993). Two types of models were developed: (1) instantaneous models which related plant biomass to environmental measurements made at the time of biomass sampling, and (2) integrated models which related cross-sectional biomass and percent bottom cover to summer channel speed.

Multiple regression was performed using the technique of backward elimination to quantify the relationship between submerged macrophyte biomass and instantaneous measures of depth, current speed, sediment exchangeable N and P concentrations and sediment grain size. Because high intercorrelation between independent variables can lead to spurious conclusions regarding the significance

of independent variables in regression models (Zar 1984), tests for collinearity were performed by analyzing the tolerance of independent variables, where tolerance is defined as 1 - R_i^2 and R_i is the multiple correlation coefficient when the *i*th independent variable is predicted from the other independent variables (Norusis 1993). Models predicting biomass from environmental factors were rejected if independent variables were collinear. Biomass values were transformed by log(biomass + 1) prior to regression analysis to stabilize variance and to allow inclusion of null values (Zar 1984). To validate the instantaneous multiple regression model, data on above-ground macrophyte biomass, water depth, current speed, sediment exchangeable N and P concentrations and sediment grain size were collected in August 1993 for 16 randomly-selected near shore sites in the Upper, Middle and Lower Nechako following the methods of the 1992 survey. All sampling and analytical methods were the same for the 1992 survey except for the analysis of sediment particle size which was performed by hydrometer analysis for particles < 70 μm and wet-sieving analysis for particles > 70 μm. Observed biomasses for the 1993 survey were then compared to biomasses predicted from the multifactor model developed with the 1992 survey data.

Integrated models were developed relating cross-sectional biomass and percent bottom cover to mean summer channel speed. Cross-sectional biomass ($g \cdot m^{-2}$) is defined as the total mass of macrophytes along a 1-m wide band extending across the channel, divided by the mean summer width of the channel. The total mass of macrophytes across the channel was determined by planimetry from graphs of biomass versus distance across the channel. Mean summer width at each of the 26 sites was estimated for the various discharge scenarios following the approach described earlier for estimating channel speed, namely curves relating river width to channel speed were developed for the three discharge gauging stations on the river (Fig. 3) and these curves were then calibrated for the 26 sites. Percent bottom cover is defined as the distance across the riverbed occupied by

macrophytes divided by the river width (× 100). As plants never colonized the centre of the channel, the maximum distance of macrophyte colonization from each riverbank was summed for a given site and then divided by the mean summer width of the site. Models relating cross-sectional biomass or bottom cover to channel speed were power functions of the form:

$$Y = A \cdot Speed^{N} \quad (4)$$

where Y is either cross-sectional biomass ($g \cdot m^{-2}$) or bottom cover (%), A is the intercept of the fitted curve, speed is mean summer (June 15 - August 15) channel speed and N is the slope of the fitted curve (Spain 1982). The equation variables were estimated iteratively (after Norusis 1993) using non-linear regression for each dependent variable until the lowest possible residual sum of squares was attained.

To predict macrophyte biomass and percent bottom cover in the Nechako River prior to Kenney Dam completion (i.e., prior to 1952) and under future discharge scenarios following the second stage of impoundment, mean summer channel speeds for the various discharge scenarios (Table 1) were input into the integrated model equations. Summer channel speeds fell outside the bounds of the integrated model equations (i.e., < 0.5 $m \cdot s^{-1}$) for six sites under the regime II scenario and one site under the regime I scenario (Table 1). To avoid over-predicting bottom cover and cross-sectional biomass for these sites, predicted bottom cover was capped at 100% and cross-sectional biomass was capped at 500 $g \cdot m^{-2}$ (the average biomass across the near-shore zone for the site with the greatest macrophyte abundance).

Results

Macrophyte community structure in the Nechako River

Fourteen taxa were observed in the Nechako River: *Elodea canadensis* Rich., *Limosella aquatica* L., *Ranunculus aquatilis* L., *Polygonum amphibium* L., *Myriophyllum exalbescens* Fern., *Callitriche hermaphroditica* L., *Ceratophyllum demersum* L., *Sagittaria cuneata* Sheld., *Elatine triandra* Schk., *Potamogeton berchtoldii* Fieb., *Potamogeton gramineus* L., *Potamogeton pectinatus* L., *Potamogeton richardsonii* (Bennett) Rydb., *Chara* and one or more moss species. *E. canadensis* was the dominant species, representing 64% of the total biomass in the river, followed by *P. richardsonii* (12%), *M. exalbescens* (5%), *P. berchtoldii* (5%) and *C. demersum* (3%). The remaining taxa comprised less than 11% of the total macrophyte biomass.

Alpha diversity was not correlated ($P > 0.05$) with mean summer channel speed (Fig. 4). However, species richness was negatively correlated with mean summer channel speed ($r = -0.66$, $P < 0.0001$) such that richness decreased from 11 at 0.5 $m \cdot s^{-1}$ to 0 at 1.8 $m \cdot s^{-1}$ (Fig. 4). Species dominance varied with instantaneous current speed (Fig. 5). At current speeds $\leq$ 0.40 $m \cdot s^{-1}$ the macrophyte community was dominated by *E. canadensis*, *P. richardsonii*, *M. exalbescens* and *P. berchtoldii*, whereas at current speeds between 0.40 and 0.60 $m \cdot s^{-1}$ the community was dominated by *R. aquatilis*, followed by *E. canadensis* and *M. exalbescens*. At current speeds > 0.60 $m \cdot s^{-1}$ the macrophyte community was primarily composed of mosses (Fig. 5).

Environmental conditions and macrophyte community biomass

Total macrophyte biomass in the Nechako River ranged from 0 to 1262 $g \cdot m^{-2}$ (dry weight), and averaged 119±20 $g \cdot m^{-2}$ (mean±1 S.E.) with a median value

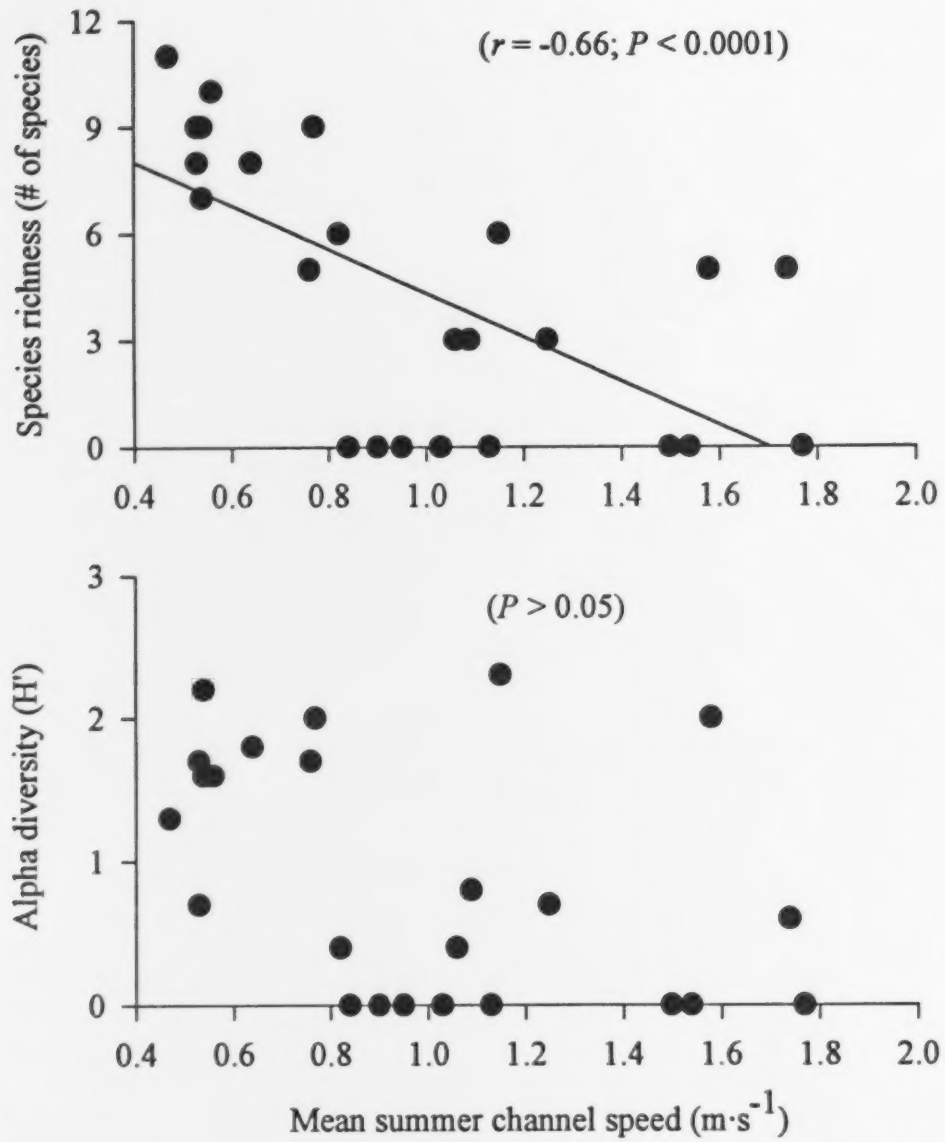

FIGURE 4. Relationship between macrophyte species diversity (alpha diversity, H'), species richness (# of species) and mean summer channel speed ($m \cdot s^{-1}$) in the Nechako River, British Columbia. NOTE: only vascular plants used in calculations of species diversity. Only 25 sites shown because one site was inhabited by mosses only (only 24 points visible because two points are superimposed).

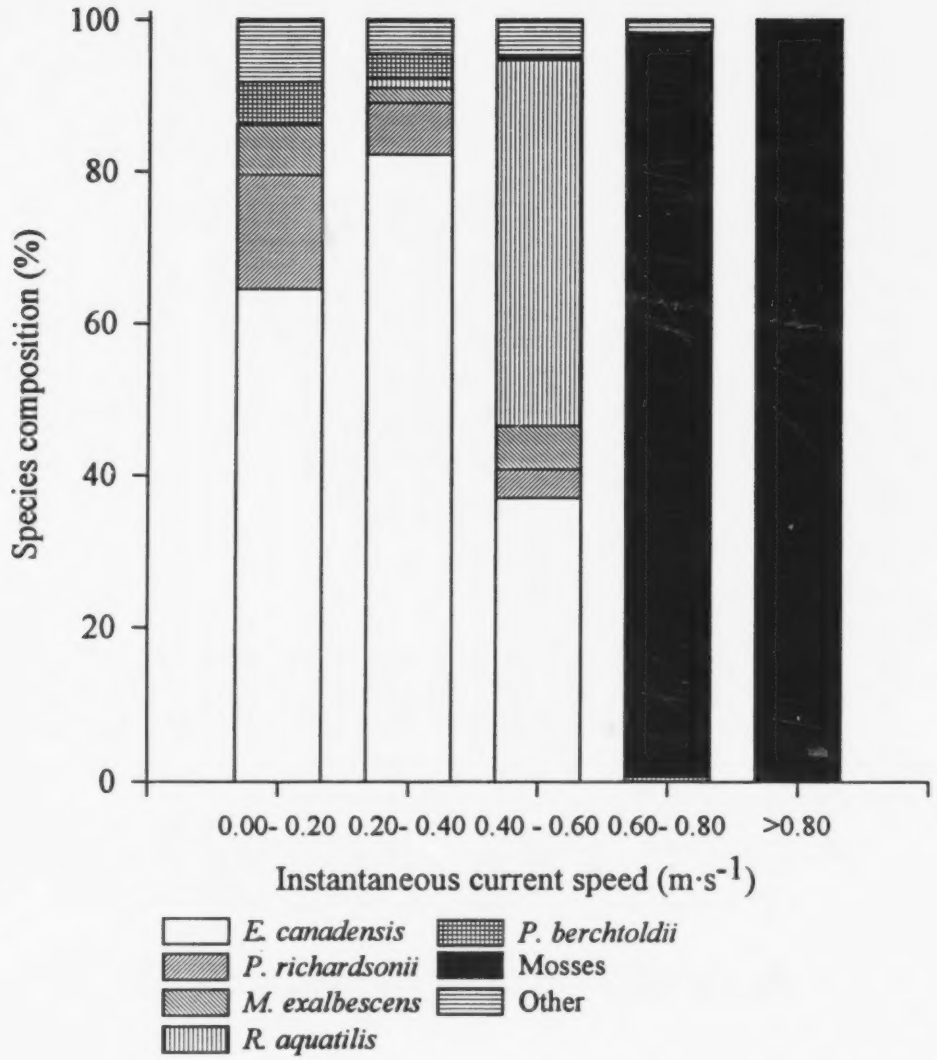

FIGURE 5. Species composition (% biomass) of macrophyte community in relation to current speed ($m \cdot s^{-1}$) in the Nechako River, British Columbia.

of 8 $g \cdot m^{-2}$ (n = 131). Highest biomasses (560 $g \cdot m^{-2}$; 95th percentile) occurred at moderate depths (0.6 - 2.3 m), low current speeds (0.00-0.20 $m \cdot s^{-1}$) and on silty sediments (14.9 - 31.2 μm) with high exchangeable P (379 - 993 $\mu g \cdot g^{-1}$) and N (41 - 63 $\mu g \cdot g^{-1}$) content (Fig. 6). Macrophyte biomass was minimal at depths > 3.0 m, on coarse sediments (> 200 μm) and in fast currents (> 0.50 $m \cdot s^{-1}$) (Fig. 6).

Total biomass was positively correlated with sediment exchangeable N (r = 0.51; $P < 0.0001$) and P (r = 0.61; $P < 0.0001$) content and negatively correlated with instantaneous current speed (r = -0.80; $P < 0.0001$), depth (r =-0.30; P = 0.01) and sediment grain size (r = -0.68; $P < 0.0001$). While no single environmental factor was a strong predictor of biomass in the Nechako River, depth, grain size and current speed together accounted for 71% of the variation in biomass (Table 2; Fig. 7). The best equation predicting biomass from instantaneous environmental factors was:

$$\log (\text{Biomass} + 1) = 2.98 - 3.70\text{Velocity} - 0.002\text{Grain size} - 0.13\text{Depth} \quad (5)$$
$$(r^2 = 0.71;\ P < 0.0001)$$

where Biomass is $g \cdot m^{-2}$, Velocity is $m \cdot s^{-1}$, Grain size is μm and Depth is m. Validation of this model with data collected from 16 sites in 1993 showed a good match between predicted-observed values for the independent data set (Fig. 7).

Sediment exchangeable P and N concentrations decreased with increasing grain size. Thus, exchangeable P concentrations were 608 $\mu g \cdot g^{-1}$ at 14 μm and 117 $\mu g \cdot g^{-1}$ at 470 μm while exchangeable N concentrations were 38 $\mu g \cdot g^{-1}$ and 5 $\mu g \cdot g^{-1}$ for the same range in grain size (Fig. 8).

Effects of river impoundment on macrophyte abundance

Bottom cover in the Nechako River ranged from 0 to 46%, averaging 12±3% with a median of 8% (n = 26; Fig. 9). Mean bottom cover was similar (P > 0.05; Tukey-HSD) for the Mid-I (2±1%; n = 9) and Lower (6±3%; n = 8) Nechako. However, the Mid-II Nechako had higher (28±3%; n = 7) macrophyte

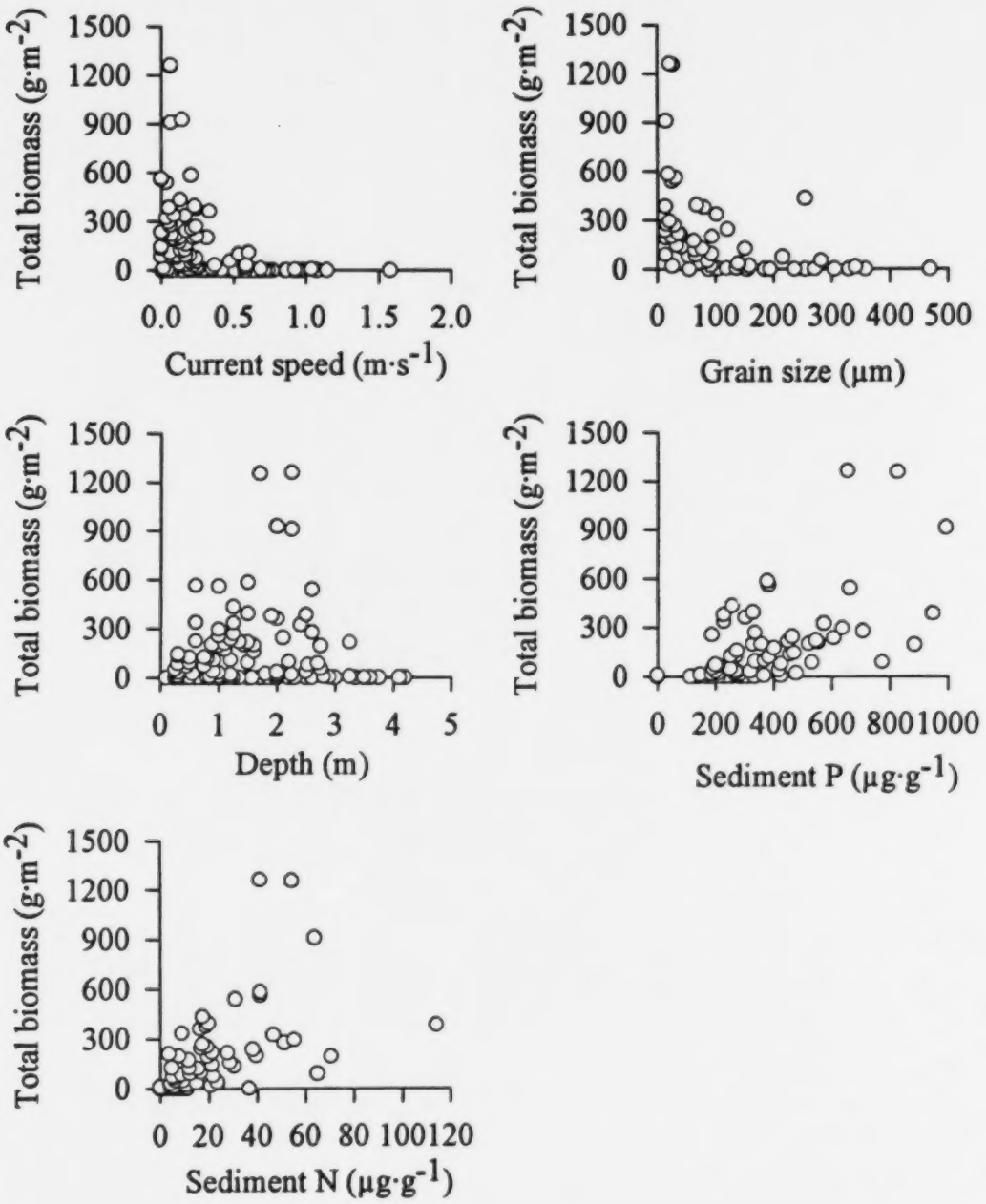

FIGURE 6. Relationship between total macrophyte biomass ($g \cdot m^{-2}$) and current speed ($m \cdot s^{-1}$), sediment grain size (µm), depth (m), and sediment exchangeable nitrogen and phosphorus ($\mu g \cdot g^{-1}$ dry weight) content in the Nechako River, British Columbia.

TABLE 2. Summary statistics and error analysis for multifactor model predicting macrophyte biomass ($g \cdot m^{-2}$) in the Nechako River, British Columbia, from depth (m), sediment grain size (μm) and current speed ($m \cdot s^{-1}$).

Independent variable	B (coefficient)	Standard error of B	95% confidence interval of B	Partial *r*	Tolerance	Significance
depth (m)	-0.13	0.07	-0.28 to 0.02	0.13	0.96	0.088
Grain size (μm)	-0.002	0.0009	-0.004 to -0.0006	-0.20	0.58	0.01
Current speed ($m \cdot s^{-1}$)	-3.70	0.61	-4.92 to -2.48	-0.31	0.58	< 0.0001
(Constant)	2.98	0.17	2.64 to 3.31	-	-	< 0.0001

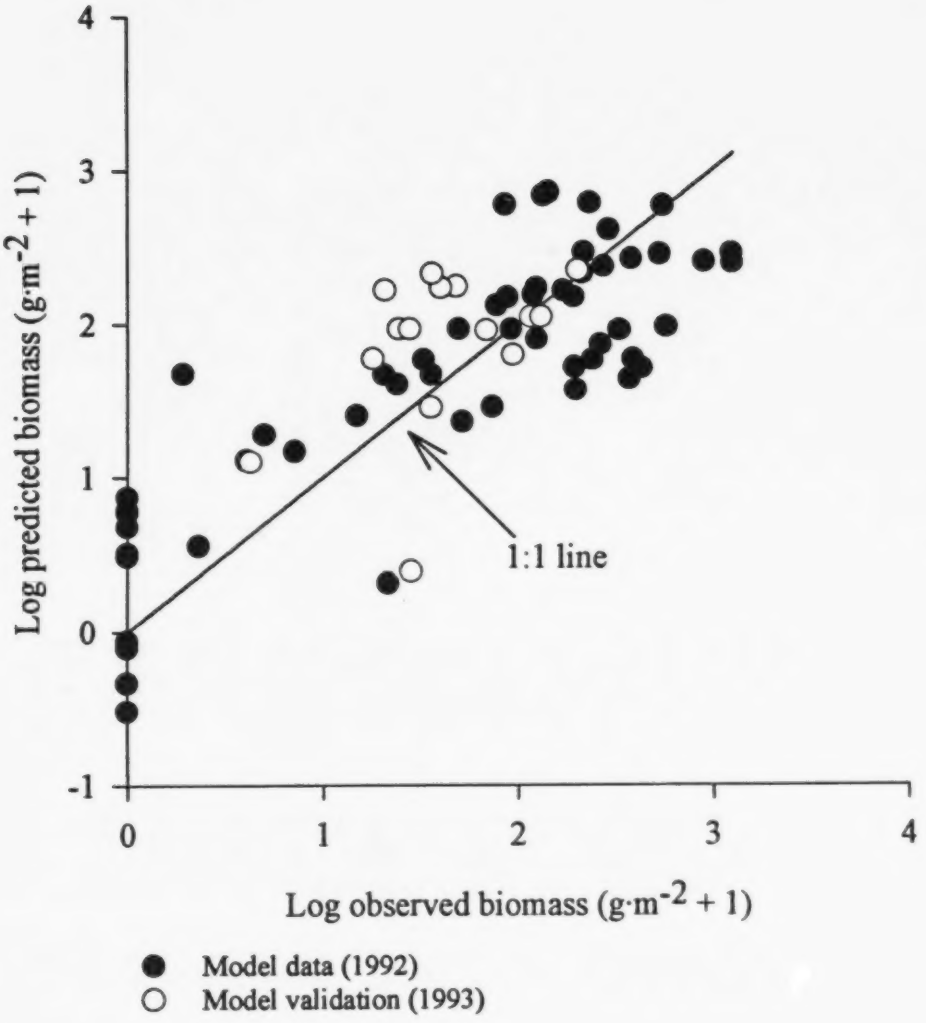

FIGURE 7. Relationship between predicted and observed macrophyte biomass ($g \cdot m^{-2}$) for the multifactor model predicting total biomass from depth (m), sediment grain size (μm) and current speed ($m \cdot s^{-1}$) for the Nechako River, British Columbia. Data from the 1993 model validation survey are shown.

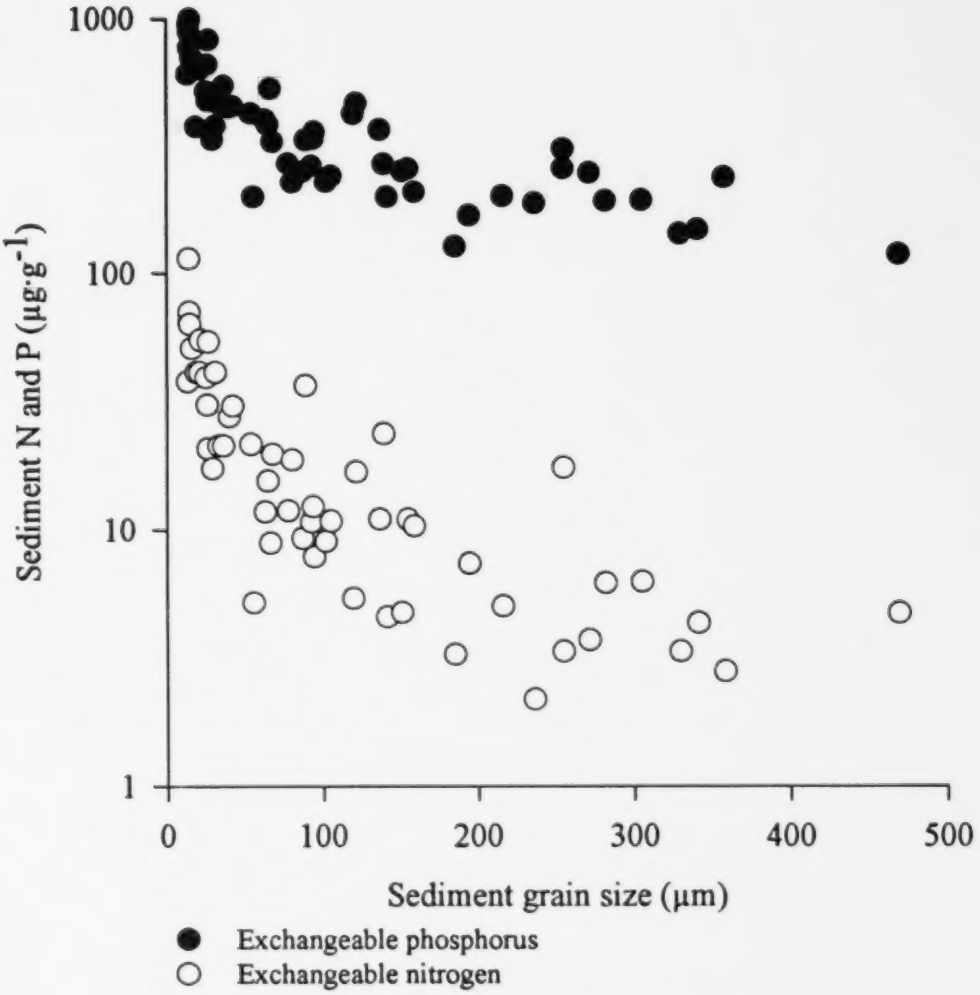

FIGURE 8. Relationship between sediment grain size (µm) and sediment exchangeable nitrogen and phosphorus ($\mu g \cdot g^{-1}$ dry weight) concentration for the Nechako River, British Columbia.

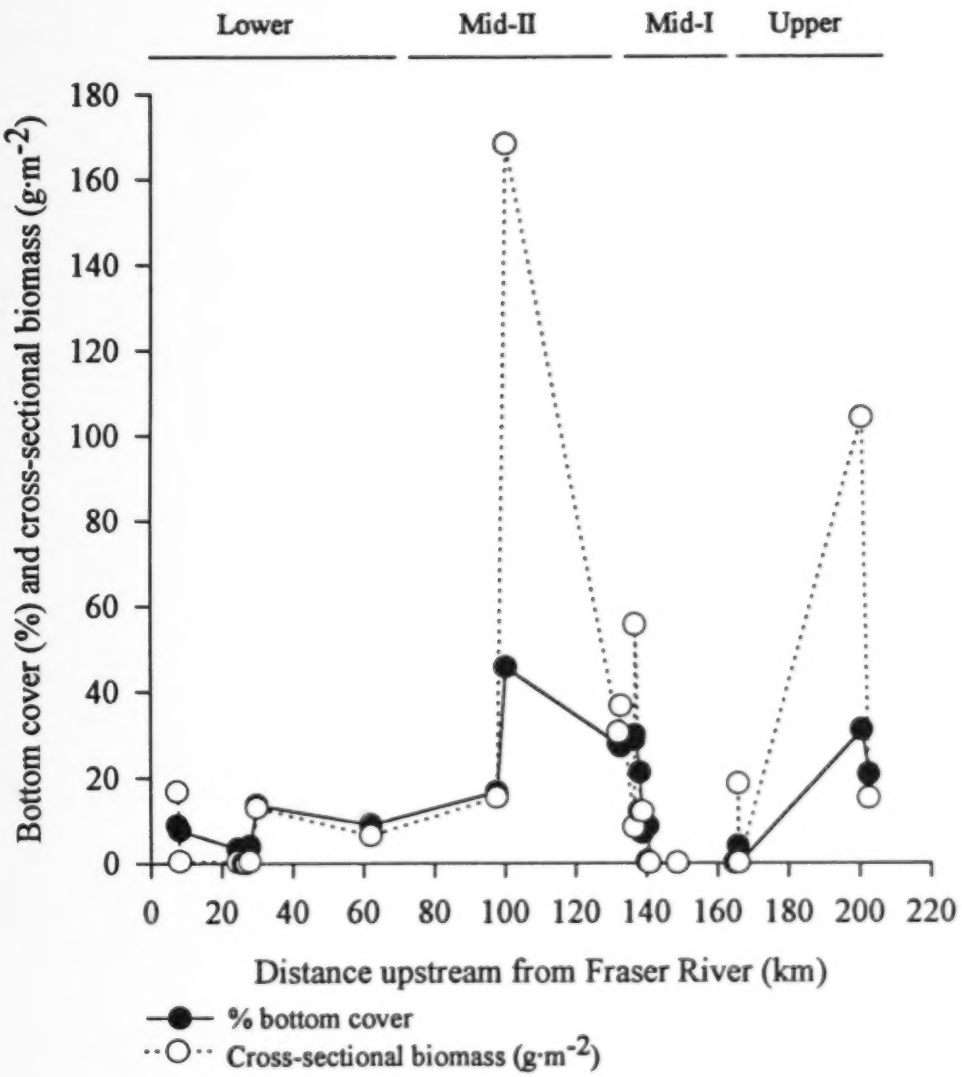

FIGURE 9. Bottom cover (%) and cross-sectional biomass ($g \cdot m^{-2}$) for 26 sites on the Nechako River, British Columbia (August 1992).

cover ($P < 0.0001$; ANOVA) (Fig. 9). Bottom cover for the two sites in the Upper Nechako was 26±5%. Cross-sectional biomass ranged from 0 to 168 $g \cdot m^{-2}$, averaging 20±7 $g \cdot m^{-2}$. Cross-sectional biomass varied between reaches ($P = 0.02$; ANOVA), averaging 4±2 $g \cdot m^{-2}$ for the Lower Nechako and 47±21 and 4±3 $g \cdot m^{-2}$ for the Mid-II and I reaches, respectively (Fig. 9). Cross-sectional biomass for the two sites in the Upper Nechako was 60±44 $g \cdot m^{-2}$.

Bottom cover decreased with increasing mean summer channel speed such that bottom cover was 46% at 0.5 $m \cdot s^{-1}$ and 3.2% at 1.8 $m \cdot s^{-1}$ (Fig. 10). The equation predicting bottom cover (%) from mean summer channel speed ($m \cdot s^{-1}$) was:

$$\text{Bottom cover} = 5.86 \cdot \text{Speed}^{-2.62} \qquad (6)$$

$$r^2 = 0.80,\ n = 26,\ F = 8.75\ (0.001 < P < 0.0025)$$

Cross-sectional biomass also decreased with increasing mean summer channel speed such that cross-sectional biomass was 168.2 $g \cdot m^{-2}$ at 0.5 $m \cdot s^{-1}$ and ~ 0 $g \cdot m^{-2}$ at 1.8 $m \cdot s^{-1}$ (Fig. 11). The equation predicting cross-sectional biomass ($g \cdot m^{-2}$) from mean summer channel speed ($m \cdot s^{-1}$) was:

$$\text{Cross-sectional biomass} = 0.15 \cdot \text{Speed}^{-9.83} \qquad (7)$$

$$r^2 = 0.82,\ n = 26,\ F = 73.0\ (P < 0.0005)$$

Predictions of bottom cover from Equation 6 indicate that since the completion of the Kenney Dam in 1952, macrophyte cover in the Upper and Mid-II reaches of the Nechako River has increased from 14±0 to 36±4% and from 10±2 to 29±5%, respectively (Fig. 12). By comparison, bottom cover appears to have changed little in the Lower and Mid-I reaches since the completion of the Kenney Dam (from 1.2±0.1 to 1.8±0.2% and from 3.8±0.4 to 6.3±0.7%, respectively). Reductions in summer discharge from the present (~ 165 $m^3 \cdot s^{-1}$) to 120 or 60 $m^3 \cdot s^{-1}$ (at Fort Fraser; Table 1) will likely increase bottom cover, particularly in the Mid-II and Upper Nechako where cover could increase by nearly 3-fold compared to present conditions (Fig. 12).

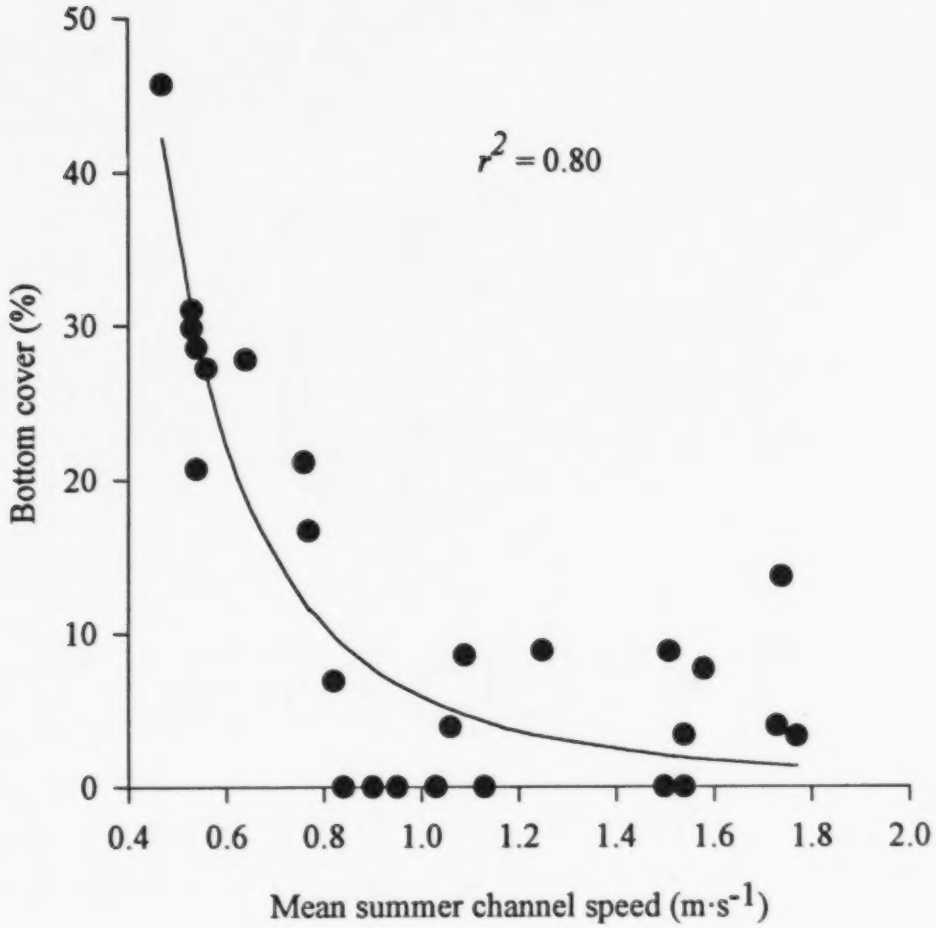

FIGURE 10. Relationship between bottom cover (%) and mean summer (June 15 - August 15) channel speed ($m \cdot s^{-1}$) for the Nechako River, British Columbia.

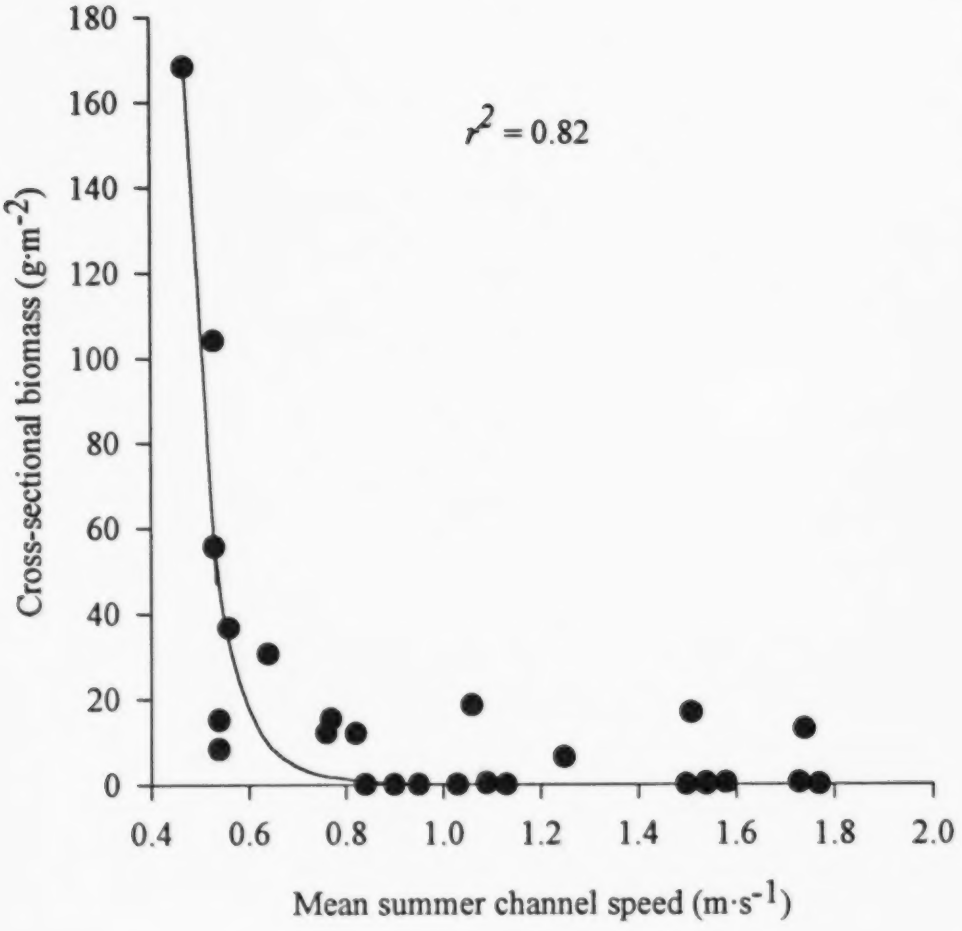

FIGURE 11. Relationship between cross-sectional biomass ($g \cdot m^{-2}$) and mean summer (June 15 - August 15) channel speed ($m \cdot s^{-1}$) for the Nechako River, British Columbia.

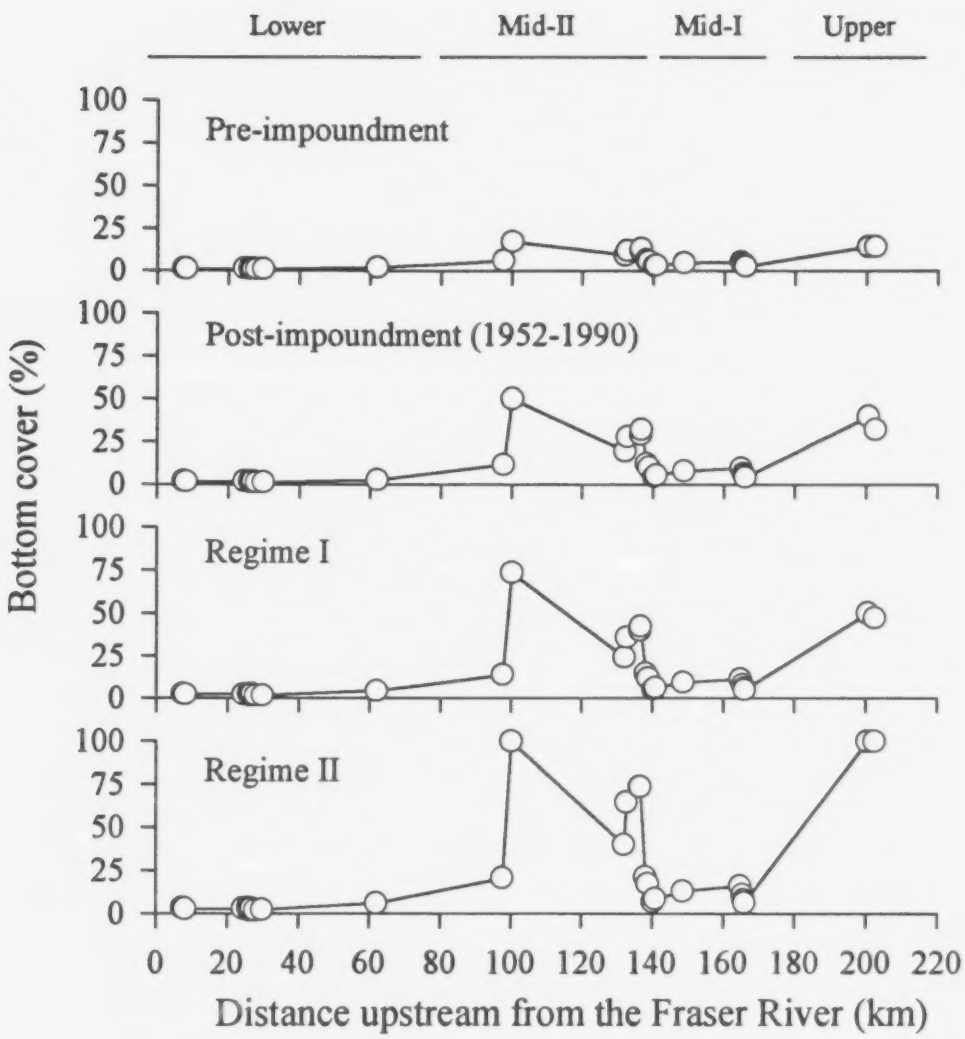

FIGURE 12. Predicted bottom cover (%) for the Nechako River, British Columbia, at various summer discharge regimes: (1) pre-impoundment (407 $m^3 \cdot s^{-1}$; long-term mean summer discharge prior to impoundment in 1952); (2) post-impoundment (165 $m^3 \cdot s^{-1}$; long-term mean summer discharge since 1952); (3) Regime I (120 $m^3 \cdot s^{-1}$) and (4) Regime II (60 $m^3 \cdot s^{-1}$).

Predictions of cross-sectional biomass from Equation 7 indicate that changes in cross-sectional biomass have been negligible in the Lower and only slight in Mid-I (0.05±0.02 $g \cdot m^{-2}$ predicted prior to 1952 versus 0.37±0.14 $g \cdot m^{-2}$ predicted for post-KDC) reaches of the Nechako since impoundment in 1952 (Fig. 13). However, predictions based on Equation 7 suggest that the impoundment of the Nechako River in 1952 resulted in substantial increases in biomass in the Mid-II and Upper reaches, with average cross-sectional biomasses increasing from 2.2±0.9 to 68.0±41.4 $g \cdot m^{-2}$ (a 31-fold increase) and from 3.6±0.0 to 101.8±36.3 $g \cdot m^{-2}$ (a 28-fold increase) in these two reaches, respectively, following impoundment (Fig. 13). Further reductions in discharge will likely result in a large expansion in macrophyte abundance in these reaches, such that at the lowest (60 $m^3 \cdot s^{-1}$, Table 1) discharge scenario cross-sectional biomass could increase by more than 12 times the current levels (Fig. 13). In contrast, there will likely be no detectable change in cross-sectional biomass in the Lower Nechako even under the most severe discharge reduction scenario (Fig. 13).

Discussion

Total community biomass in the Nechako River was positively correlated with sediment exchangeable N (r = 0.51) and P (r = 0.61) concentrations and negatively correlated with current speed (r = -0.80), depth (r = -0.30) and sediment grain size (r = -0.68). A multifactor model combining depth, grain size and current speed (Equation 5) best accounted for variation in community biomass in the Nechako River (r^2 = 0.71), with current speed being the most influential environmental factor (partial r = -0.31), followed by grain size (partial r = -0.20) and depth (partial r = -0.13; Table 2). The observation that current speed is the primary environmental factor affecting the biomass of riverine macrophytes is

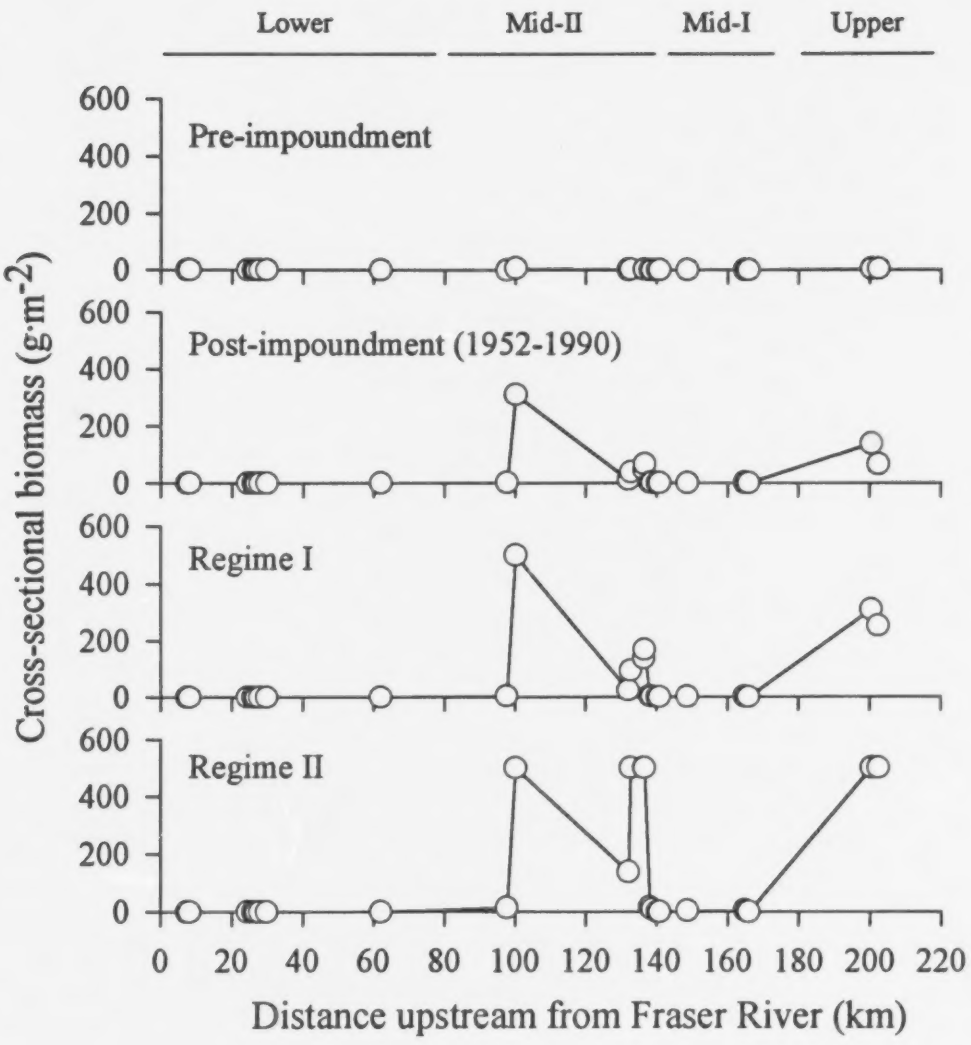

FIGURE 13. Predicted cross-sectional biomass ($g \cdot m^{-1}$) for the Nechako River, British Columbia, at various summer discharge regimes: (1) pre-impoundment (407 $m^3 \cdot s^{-1}$; long-term mean summer discharge prior to impoundment in 1952); (2) post-impoundment (165 $m^3 \cdot s^{-1}$; long-term mean summer discharge since 1952); (3) Regime I (120 $m^3 \cdot s^{-1}$) and (4) Regime II (60 $m^3 \cdot s^{-1}$).

consistent with Chambers *et al.* (1991) who found that aquatic macrophyte biomass was significantly ($P < 0.0005$) and inversely correlated ($r > -0.68$) with current speed over the range 0.01-1 $m \cdot s^{-1}$ in the Bow River, Alberta. Furthermore, Chambers *et al.* (1991), using an experimental approach *in situ*, showed that the growth rate of *P. pectinatus* decreased with increasing current speed over the range 0.2-0.7 $m \cdot s^{-1}$, irrespective of changes in sediment properties. While few studies have investigated the mechanism by which sediment grain size affects the growth of macrophytes, the increase in biomass with decreasing grain size may relate to the observation that finer sediments tend to have higher nutrient (e.g., nitrogen and phosphorus) content than coarser sediments (Fig. 8).

In addition to being an important determinant of total biomass, current speed is also an important environmental factor controlling the species composition of macrophyte communities. Thus, *E. canadensis* was the dominant species in regions of the Nechako River with current speeds < 0.40 $m \cdot s^{-1}$, whereas *R. aquatilis* dominated regions of moderate current speed (0.40 - 0.60 $m \cdot s^{-1}$), while mosses predominated in regions with current speeds > 0.60 $m \cdot s^{-1}$ (Fig. 5). The changes in species dominance along the current speed gradient may be attributable to the growth form of the dominant species. The "bushy" morphology of *E. canadensis* may be better adapted to slow-flowing environments, whereas the spindly and cushion-like growth forms of *R. aquatilis* and mosses, respectively, may be better suited to fast current speeds. Although species richness was negatively correlated with mean summer channel speed ($r = -0.66$, $P < 0.0001$), species diversity was not related to channel speed indicating that at low channel speeds where richness may be high, many species may be present in very low biomass and may not contribute significantly to the overall complexity of the stand (Fig. 4).

While the multifactor model based on instantaneous measures of current speed, depth and sediment grain size was a good predictor of macrophyte biomass,

it would not allow predictions of biomass under future discharge scenarios due to the difficulty in obtaining realistic input values for instantaneous independent variables. To allow predictions of macrophyte abundance under future discharge scenarios, empirical models were developed relating cross-sectional biomass and bottom cover to mean summer channel speed (equations 6 and 7), where mean summer channel speed was approximated for discharge regimes from discharge-channel speed relationships (Fig. 3). The models predict that, relative to current conditions, macrophyte biomass and bottom cover in the Mid-II reach of the Nechako was 31- and 3-fold less, respectively, prior to regulation (i.e., prior to 1952) and will increase up to 3- and 12-fold, respectively, if mean summer discharge in the Upper Nechako is reduced to 60 $m^3 \cdot s^{-1}$ (Figs. 12 and 13). In contrast, the Lower and Mid-I reaches appear to have had little change in macrophyte abundance since regulation and will likely experience very little change in macrophyte abundance (Figs. 12 and 13) even at the lowest discharge scenario (60 $m^3 \cdot s^{-1}$).

The predictions of increased macrophyte abundance following completion of the Kenney Dam in 1952 and further increases in the event of a future second impoundment are consistent with observations from other regulated river systems (Table 3). For example, Attwell (1970) and Jackson and Davies (1976) reported that the lack of flushing discharges in the Zambezi River, Rhodesia, resulted in substantial increases in *Salvinia auriculata*, *Pistia stratiotes*, *Panicum repens* and *Phragmites mauritianus* to the point where they are "clogging" the river. Similarly, Rorslett *et al.* (1989) reported that regulation of the Suldalslagen River, Borsleva River and Otra River (all of Norway) has resulted in large increases in aquatic macrophyte abundance to the point where sections of the Borsleva River are choked by dense growths of *Potamogeton alpinus* and the submerged moss *Fontinalis antipyretica* (Table 3). While it is clear that river regulation practices can result in large increases in aquatic macrophyte abundance, the

TABLE 3. Examples of rivers in which macrophyte communities have reportedly changed since impoundment.

Name of river	Nature of change in macrophyte community	Taxa involved in change	References
Tees River, England	substantial* increase	*Potamogeton crispus, Zannichellia palustris, Myriophyllum spicatum*	Holmes and Whitton (1977)
Mill Creek, Wisconsin, U.S.A.	increase to 100% cover, followed by levelling out at 30-50% cover (slightely greater than background)	*Elodea canadensis, P. crispus, Potamogeton foliosus, Ranunculus trichophyllus*	Hilsenhoff (1971)
Umealven River, Sweden	increase in the number of species from ~ 13 (before impoundment) to 39 (following impoundment)	numerous new species present following impoundment	Nilsson (1978)
Zambezi River, Rhodesia	substantial increases ("clogging river")	*Salvinia auriculata, Pistia stratiotes, Panicum repens, Phragmites mauritianus*	Attwell (1970), Jackson and Davies (1976)
Otra River, Norway	substantial increases	*Juncus bulbosus* (up to 55% surface coverage)	Rorslett *et al.* (1989)
Suldalslagen River, Norway	significant increases (up to 100% coverage)	Bryophytes, *Callitriche humulata, J. bulbosus*	Rorslett *et al.* (1989)
Borsleva River, Norway	substantial increases	*Carex rostrata* and *Equisetum fluviatile* (helophytes), *Potamogeton alpinus, Fontinalis antipyretica* (bryophyte)	Rorslett *et al.* (1989)
Tuolumne River, California, U.S.A.	substantial increases	*Eichhornia crassipes*	Fraser (1972)
Dordogne River, France	substantial increases	*Ranunculus fluitans*	Décamps *et al.* (1979)
Truyere River, France	substantial increases	*Ranunculus fluitans* var *peltatus*	Décamps *et al.* (1979)
Tennessee River, U.S.A.	substantial increases	*Potamogeton* spp.	Krenkel *et al.* (1979)
Sutlej River, India	substantial increases	?	Petts (1984)
Colne River, Britain	increases	?	Butcher (1933)
Rheidel River, Western Europe	substantial increases	*Callitriche* spp., *Ranunculus* spp.	Haslam (1987)
Volta River, Ghana	substantial increases	*Vallisneria aethiopica, Potamogeton actandrus*	Petts (1984)

* most studies investigating the effects of river impoundment on macrophyte communities do not provide precise estimates of change.

mechanisms by which macrophytes proliferate following regulation are not obvious. Rorslett *et al.* (1989), in case studies of the Otra, Suldalslagen and Borsleva Rivers, suggests two possible mechanisms: (1) enhanced growths following winter flow increases with coinciding summer flow decreases, and (2) enhanced growths following an overall flow reduction. Increases in winter flows in the Otra River from ~ 40 to ~ 70 $m^3 \cdot s^{-1}$ keeps the river ice-free downstream of the power plant, thereby increasing the growing season of aquatic macrophytes. In addition, decreased summer flows in the Otra River promoted further expansion of macrophyte communities (Rorslett *et al.* 1989). While regulation of the Otra River has resulted in increased winter flows and decreased summer flows, regulation of the Suldalslagen (which currently has average annual flows < 55% pre-regulation levels) and Borsleva rivers has resulted in overall reduction in average streamflow, such that sections of the Borsleva River have become chains of stagnant pools interspersed with wetlands (Rorslett *et al.* 1989). Data presented in this study suggest that flow reductions may promote expansions of macrophyte communities by slowing channel velocities (which are positively correlated with discharge).

Increases in macrophyte abundance following impoundment has often been associated with changes in other trophic levels. For example, increases in *Eichhornia crassipes* following the impoundment of the Tuolumne River, California, impaired and in some cases totally blocked salmonid migration (Fraser, 1992). Similarly, Rorslett *et al.* (1989) reported that the increase in macrophyte abundance following the impoundment of the Suldalslagen River, southwestern Norway, caused a substantial decrease in salmonid production because the nature of the riverbed became unfit for spawning. In the River Wye, Wales, the decomposition of extensive macrophyte beds (36% coverage) combined with high water temperatures (28 °C) resulted in severe deoxygenation (as low as 0.5 $mg \cdot L^{-1}$) of the water column and coincided with a major die-off of salmonids in 1976. Likewise, Attwell (1970) reported that the increase in macrophyte abundance

associated with the impoundment of the Zambezi River negatively affected hippopotamus, crocodile and various waterfowl populations. Impoundment of the Otra River, Norway, has encouraged the growth of macrophytes to the point where boating and angling have been adversely affected while in certain areas the landing of small aircraft is no longer possible due to the presence of dense macrophyte communities (Rorslett *et al.* 1989). Given that the Nechako River is an important migration corridor for salmonids (Bradford, 1994), is valued for recreational sports and serves as a water source for towns and irrigators, excessive growths of macrophytes which may occur with further discharge reduction may have detrimental effects on the river's salmonid production capability, recreational potential and water quality.

In conclusion, this study showed that aquatic macrophyte biomass in the Nechako River is positively correlated with sediment exchangeable N and P concentrations, and negatively correlated with depth, current speed and sediment grain size. In addition to being an important determinant of total biomass, current speed was also shown to be an important environmental factor controlling the species composition of macrophyte communities. Predictions of macrophyte biomass and cover based on mean summer channel speed indicate macrophyte abundance has increased in the Upper and Mid-II Nechako River since initial impoundment in 1952 and may increase yet again under plans to further reduce flows in the river. Given the ecological importance of macrophytes in riverine environments and the extent of dam-building activities world-wide, it is critical that environmental managers be able to quantify the effect of environmental factors on macrophyte abundance and thus predict changes in submerged macrophyte abundance in response to river regulation and other environmental manipulations.

References Cited

ATTWELL, R. I. G. 1970. Some effects of Lake Kariba on the ecology of a floodplain of the Mid- Zambezi Valley of Rhodesia. Biol. Conserv. **2:** 189-196.

BARBOUR, M. G., J. H. BURK, AND W. D. PITTS. 1987. Terrestrial plant ecology, (2nd edition). The Benjamin/Cummings Publishing Company, Inc., Don Mills, Ontario 634 pp.

BARKO, J. W., AND R. M. SMART. 1981. Sediment-based nutrition of submersed macrophytes. Aquat. Bot. **10:** 339-352.

BILBY, R. 1977. Effects of spate on the macrophyte vegetation of a stream pool. Hydrobiologia **56:** 109-112.

BOYD, C. E. 1970. Chemical analyses of some vascular aquatic plants. Arch. Hydrobiol. **67:** 78-85.

BRADFORD, M. J. 1994. Trends in the abundance of Chinook Salmon (*Oncorhynchus tshawytscha*) of the Nechako River, British-Columbia. Can. J. Fish. Aquat. Sci. **51:** 965-973.

BREMNER, J. M. 1965. Inorganic forms of nitrogen, p. 1179-1237. *In* C. A. Black [Ed.], Methods of Soil Analysis. American Society of Agronomy; Inc., Madison, WI. 1572 p.

BRITISH COLUMBIA DEPARTMENT OF ENERGY, MINES AND RESOURCES. 1977. Surveys and Mapping Branch. 1:50000 Maps, British Columbia.

BROOKER, M. P., D. L. MORRIS, AND R. J. HEMSWORTH. 1977. Mass mortalities of adult salmon (*Salmo salar*) in the River Wye, 1976. J. Appl. Ecol. **14:** 409-417.

BUSCEMI, P. P. 1958. Littoral oxygen depletion produced by a cover of *Elodea canadensis*. Oikos **9:** 239-245.

BUTCHER, R. W. 1933. Studies on the ecology of rivers. I. On the distribution

of macrophytic vegetation in the rivers of Britain. J. Ecol. **21:** 58-91.

CATTANEO, J., AND J. KALFF. 1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. Limnol. Oceanogr. **25:** 280-289.

CHAMBERS, P. A., J. M. HANSON, J. M. BURKE, AND E. E. PREPAS. 1990. The impact of the crayfish *Orconectes virilis* on aquatic macrophytes. Freshwater Biol. **24:** 81-91.

CHAMBERS, P. A., E. E. PREPAS, H. R. HAMILTON, AND M. L. BOTHWELL. 1991. Current velocity and its effect on aquatic macrophytes in flowing water. Ecol. Appl. **1:** 249-257.

CHITTENDEN, E. T., C. W. CHILDS, AND R. E. SMIDT. 1976. Sediments of Lake Rotoroa, South Island, New Zealand. N. Z. J. Mar. Freshw. Res. **10:** 61-76.

DÉSCAMPES, H. J., H. CAPBLANCQ, H. CASONOVA, AND T. J. TORENQ. 1979. Hydrobiology of some regulated rivers in the southwest of France. *In* J. W. Ward, and J. A. Stanford [Eds.], The ecology of regulated streams. Proc. 1st Int. Symp. Reg. Streams. Plenum Press, New York.

ENVIRONMENT CANADA. 1991. Historical streamflow summary, British Columbia, to 1990. Environment Canada, Inland Waters Directorate, Water Resources Branch, Water Survey of Canada, Ottawa, Canada.

FRASER, J. C. 1972. Regulated discharge and the stream environment. *In* R. T. Oglesby, C. A. Carlson, and J. A. McCann [Eds.], 1972. River ecology and man. Proceedings of an International Symposium on River Ecology and the Impact of Man, University of Massachusetts. Academic Press, New York.

GLIME, J. M., AND D. H. VITT. 1984. The physiological adaptations of aquatic Musci. Lindbergia **10:** 41-52.

GLIME, J. M., AND D. H. VITT. 1987. A comparison of bryophyte species diversity and niche structure of montane streams and stream banks. Can.

J. Bot. **65:** 1824-1837.

GORDON, N. D., T. A. MCMAHON, AND B. L. FINLAYSON. 1992. Stream hydrology, an introduction for ecologists. John Wiley & Sons, Toronto. 526 pp.

GRAY, D. M. 1973. Handbook on the principles of hydrology: A general text with special emphasis on Canadian conditions. Secretariat, Canadian National Committee for the International Hydrological Decade.

GREGG, W. W., AND F. L. ROSE. 1982. The effects of aquatic macrophytes on the stream microenvironment. Aquat. Bot. **14:** 309-324.

HAAG, R. W., AND P. R. GORHAM. 1977. Effects of thermal effluent on standing crop and net production of *Elodea canadensis* and other submerged macrophytes in Lake Wabamun, Alberta. J. Appl. Ecol. **14:** 835-851.

HARROD, J. J. 1964. The distribution of invertebrates on submerged aquatic plants in a chalk stream. J. Anim. Ecol. **33:** 335-341.

HASLAM, S. M. 1978. River plants: the macrophytic vegetation of watercourses. Cambridge University Press, Cambridge, U. K. 396 pp.

HASLAM, S. M. 1987. River plants of western Europe. Cambridge University Press. New York. 512 pp.

HILSENHOFF, W. L. 1971. Changes in downstream insect and amphipod fauna caused by an impoundment with a hypolimnion drain. Entom. Soc. Am. Ann. **64:** 743-746.

HOLMES, N. T. H., AND B. A. WHITTON. 1977. The macrophytic vegetation of the River Tees in 1975: observed and predicted changes. Freshwater Biol. **7:** 43-60.

JACKSON, P. B. N., AND B. R. DAVIES. 1976. Cabora Basin fish in its first year: some ecological aspects and comparisons. Rhodesia Science News, 10: 128-133. *In* G. E. Petts, 1984. Impounded rivers, perspectives for ecological management. John Wiley and Sons, Toronto. 326 pp.

KREBS, C. J. 1989. Ecological methodology. Harper Collings Publishers, New York, NY. 654 pp.

KRENKEL, P. A., G. F. LEE, AND R. A. JONES. 1979. Effects of TVA impoundments on downstream water quality and biota. *In:* J. V. Ward, and J. A. Stanford [Eds.], The ecology of regulated streams. Proc. 1st Int. Symp. Reg. Streams. Plenum Press, New York.

MADSEN, T. V., AND E. WARNCKE. 1983. Velocities of currents around and within submerged aquatic vegetation. Arch. Hydrobiol. **97:** 389-394.

MAYES, R. A., A. W. MCINTOSH, AND V. L. ANDERSON. 1977. Uptake of cadmium and lead by a rooted aquatic macrophyte (*Elodea canadensis*). Ecology **58:** 1176-1180.

MCGAHA, Y. J. 1952. The limnological relations of insects to certain aquatic flowering plants. Trans. Am. Microsc. Soc. **71:** 335-381.

MCROY, C. P., AND R. J. BARSDATE. 1970. Phosphate absorption in eelgrass. Limnol. Oceanogr. **15:** 6-13.

MURPHY, J. A., AND J. L. RILEY. 1962. A modified single solution method for the determination of inorganic phosphate in natural waters. Anal. Chim. Acta. **27:** 31-36.

NILSSON, C. 1978. Changes in the aquatic flora along a stretch of the River Umealven, N. Sweden. Hydrobiologia **61:** 229-236.

NORUSIS, M. J. 1993. SPSS for Windows, Base systems user's guide, Release 6.0. SPSS Inc. 828 pp.

PETTS, G. E. 1984. Impounded rivers, perspectives for ecological management. John Wiley and Sons, Toronto. 326 pp.

PIP, E., AND J. M. STEWART. 1976. The dynamics of two aquatic plant-snail associations. Can. J. Zool. **54:** 1192-1205.

POKORNY, J., J. KVET, J. P. ONDOK, Z. TOUL, AND I. OSTRY. 1984. Production-ecological analysis of a plant community dominated by *Elodea canadensis*

Michx. Aquat. Bot. **19:** 263-292.

RAWLENCE, D. J., AND J. S. WHITTON. 1977. Elements in aquatic macrophytes, water, plankton and sediments surveyed in three North Island lakes. N. Z. J. Marine Freshw. Res. **11:** 73-93.

RORSLETT, B. 1988. Aquatic weed problems in a hydroelectric river: the R. Otra, Norway. Regul. Rivers Res. & Manage. **2:** 25-37.

RORSLETT, B., D. BERG, AND S. W. JOHANSEN. 1985. Mass invasion of *Elodea canadensis* in a mesotrophic, South Norwegian lake - impact of water quality. Verh. Int. Ver. Theor. Angew. Limnol. **22:** 2920-2926.

RORSLETT, B., M. MJELDE, AND S. W. JOHANSEN. 1989. Effects of hydropower development on aquatic macrophytes in Norwegian rivers: present state of knowledge and some case studies. Regul. Rivers Res. & Manage. **3:** 19-28.

SHELDON, S. P. 1987. The effects of herbivorous snails on submerged macrophyte communities in Minnesota lakes. Ecology **68:** 1920-1931.

SOLORZANO, L. 1969. Determination of ammonia in natural waters by phenolhypochlorite method. Limnol. Oceanogr. **14:** 799-801.

SPAIN, J. D. 1982. Basic microcomputer models in biology. Addison-Wesley Publishing Co., Reading Mass. 354 pp.

VITT, D. H., Y. YENHUNG, AND R. J. BELLAND. 1995. Patterns of bryophyte diversity in peatlands of continental western Canada. The Bryologist **98:** 218-227.

WARRINGTON, P. D. 1980. Studies on aquatic macrophytes part XXXIII: Aquatic plants of British Columbia. Province of British Columbia, Ministry of Environment, Inventory and Engineering Branch, December, 1980.

WHITEHEAD, H. 1935. An ecological study of the invertebrate fauna of a chalk stream near Great Driffield, Yorkshire. J. Anim. Ecol. **4:** 58-78.

WHITTAKER, R. H. 1972. Evolution and measurement of species diversity. Taxon **21:** 213-251.

WILLIAMS, J. D. H., J. K. SYERS, AND T. W. WALKER. 1967. Fractionation of soil inorganic phosphate by a modification of Chang and Jackson's procedure. Soil Sci. Am. Proc. **31:** 736-739.

ZAR, J. H. 1984. Biostatistical analysis (2nd edition). Prentice-Hall, Inc., Englewood Cliffs, N. J. 718 pp.

3. The role of morphometry in determining the structure (diversity and biomass) of riverine macrophyte communities[1]

Introduction

Many studies have shown that biological production in lakes is functionally linked to lake-basin (i.e., lake surface area - A_o, mean depth - $\bar{z}$, maximum depth - z_{max}, and littoral slope) and catchment (i.e., catchment area - A_d, and slope) morphometry. For example, Fee (1979) and Carpenter (1983) showed that phytoplankton production in lakes is a function of the ratio of $\bar{z}$ to z_{max}. Rasmussen and Kalff (1987), in a study of more than 100 lakes located in North America, Europe, Iceland, Japan and New Zealand, found that macrozoobenthos biomass is correlated with bottom-slope, the $\bar{z}$:z_{max} ratio and A_o. Bottom-slope has also been shown to be an important determinant of submerged macrophyte abundance such that Duarte and Kalff (1986) showed that 72% of the variability in peak macrophyte biomass was accounted for by the slope of the littoral zone in Lake Memphremagog (Quebec/Vermont). Perhaps the most well known morphometry-production studies are those that advanced the work of D. S. Rawson (1952) who related fish productivity to $\bar{z}$. These studies eventually led to the development of the popular morphoedaphic index which predicts fish abundance (yield) in north temperate lakes from total dissolved solids concentration and $\bar{z}$ (e.g., Ryder 1965; Ryder *et al.* 1974; Matuszek 1978; Ryder 1982; Youngs and Heimbuch 1982; Kerr and Ryder 1988).

It is arguable that large-scale determinants of productivity, such as morphometry, are redundant in that biotic production is more directly dependent upon proximal factors such as nutrient availability (Schindler *et al.* 1971; Dillon

[1]A version of this chapter will be submitted for publication in *Limnology and Oceanography*

and Rigler 1974; Bothwell 1992), light attenuation (Spence 1982; Chambers and Prepas 1988), temperature (Castenholz 1969; Haag and Gorham 1977) and the concentration of toxicants (Stockner and Costella 1976; Moore and Love 1977). However, there is much evidence supporting the premise that catchment and lake-basin geometry ultimately control these factors. For example, the depth of the euphotic zone, that is the portion of a lake which extends from the lake surface down to where light is about 1% of that at the surface (e.g., Wetzel 1983), is negatively correlated with water color (Spence 1982; Rasmussen *et al.* 1989), with water color being functionally dependent upon the drainage ratio (A_d:A_o), $\bar{z}$ and catchment slope (Gorham *et al.* 1983; 1986; Engstrom 1987; Rasmussen *et al.* 1989). Because water color influences the attenuation of infrared light (a major source of heat in lakes), morphometry, via its influence on water color, also affects the vertical thermal profiles of lakes. Similarly, nutrient loading to lakes and nutrient retention, both of which are related to a lake's biotic productivity, have been shown to have dependence upon morphometric variables such as A_d, A_o and $\bar{z}$ (e.g., Patalas and Salki 1973; Dillon and Rigler 1974; Kirchner and Dillon 1975). Small lakes (i.e., small A_o) are thought to produce more fish per unit area than large lakes (i.e., large A_o) because small lakes tend to have a larger proportion of their substrate within the euphotic zone and, thus, usually have proportionally larger littoral zones than large lakes, with fish production being positively correlated with littoral area (e.g., Larkin 1964; Ryder *et al.* 1974). Thus, there is much evidence supporting the concept that catchment and lake-basin morphometry play a major role in determining the production potential of lakes through their influences on abiotic regimes (i.e., nutrient availability, light attenuation, etc.).

While numerous studies have quantified biotic production in lakes in terms of morphometry few, if any, studies have related biological variables in riverine environments to morphometric properties. Since the rate of water movement (velocity) in river channels is determined by channel geometry (morphometry)

(Gray 1970; Hogan and Church 1989; Bras 1990, Gordon *et al.* 1992) and the distribution and abundance of riverine biota are highly dependent upon velocity regimes (e.g., Chapter 2 of this thesis; Hynes 1970; Nilsson 1987; Chambers *et al.* 1991), channel morphometry should, via its influence on velocity, have a major role in shaping the ecology of riverine ecosystems. The aim of this study was to test the hypothesis that macrophyte abundance (biomass and bottom cover) and community structure (species composition and diversity) are functions of both small scale (near shore cross-sectional slope) and large scale (catchment area and longitudinal slope) characteristics of river basin morphometry. To test the hypothesis that near shore slope influences macrophyte community structure, macrophyte community structure in the Nechako River, British Columbia, was related to near shore cross-sectional slope. This relationship was then compared with data for the Bow River, Alberta, Canada (Alberta Environment unpubl. data) and Lake Memphremagog, Quebec/Vermont (Duarte and Kalff 1986). Large scale morphometric characteristics of the Nechako River were also related to macrophyte community structure and compared with predictions from the river continuum (Vannote *et al.* 1980; Minshall *et al.* 1985a) and intermediate disturbance (Connell 1978; Ward and Stanford 1983) hypotheses which attempt to generalize about the structure of ecosystems in terms of environmental heterogeneity and large scale properties of drainage basins.

Methods and Materials

Study site, field sampling methods and laboratory analyses

A description of the Nechako River, British Columbia (the river system used in this study), is given in Chapter 2 ("*Study site*" section) of this thesis and, to conserve space and minimize repetition, is not repeated in this chapter. Similarly,

the methods used to collect macrophytes and analyze sediments are identical to those described in the "*Field sampling methods*" and "*Laboratory analyses*" sections, respectively, of Chapter 2 and are not repeated in this chapter.

Determination of morphometric properties

Near shore cross-sectional slope (CSS) was determined for every interval along each of the 26 transects as:

$$CSS = \frac{\Delta depth\ (m)}{\Delta distance\ (m)} \times 100 \quad (1)$$

where Δdepth is the depth of the interval minus the depth of nearest shore-side interval and Δdistance is the distance of the interval to nearest shore-side interval (usually 5 m, sometimes 10 m).

To determine longitudinal slope (i.e., slope along the upstream-downstream direction) the Nechako River was divided into three reaches: (1) Upper Nechako (Nautley River confluence to the Vanderhoof bridge) characterized by fast current speeds and shallow depths; (2) Middle Nechako (Vanderhoof Bridge to the Stuart River confluence) characterized by slow current speeds and shallow depths; and (3) Lower Nechako (Stuart River confluence to the Fraser River confluence) characterized by fast current speeds and deep water (Fig. 1). Longitudinal slope was estimated for each of these reaches by measuring the elevation above sea-level at the water's surface at the beginning and end of each reach with a precision altimeter (American Paulin System, L.A., California, Model MM-1) and then dividing the length of the reach (determined with the computer program Sigma Scan version 3.9 and 1:50000 topographic maps) into the change in elevation determined for the reach. Prior to measuring elevations along the river, the altimeter was calibrated to a geodetic landmark of known elevation in the city of Prince George. All elevation determinations were undertaken on the same day to

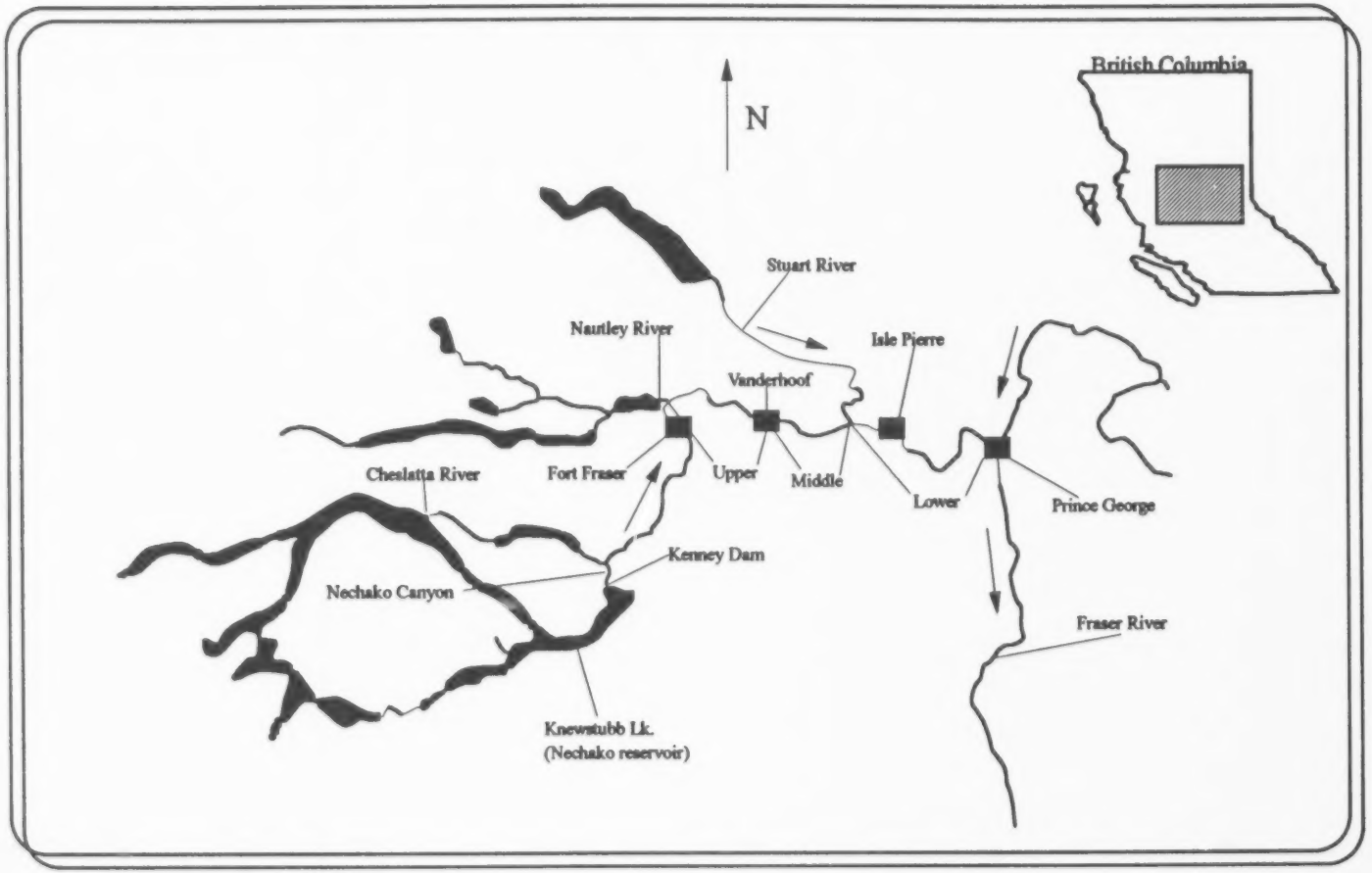

FIGURE 1. Map showing the Nechako River and area. The Nechako River flows into the Fraser River at the city of Prince George which is located near the geographical center of the province of British Columbia, Canada.

minimize errors due to fluctuations in water level.

The catchment area for the three reaches was obtained from Environment Canada (1991). For the Lower Nechako, the catchment area is ~ 42500 km^2 (measured at Isle Pierre; 53° 57' 37" N; 123° 14' 01" W), while the catchment area for the Middle Nechako is ~ 25100 km^2 (measured at Vanderhoof; 54° 01' 34" N; 124° 14' 01" W). The catchment area for the Upper Nechako was estimated by adding the catchment area for the Nechako River at Fort Fraser (~ 17700 km^2 at 54° 03' 18" N, 124° 33' 39" W) to the catchment area of the Nautley River (~ 6030 km^2 at 54° 05' 07" N, 124° 35' 58" W). Temporal variability (i.e., the difference between minimum and maximum values) in discharge increased with increasing distance from the headwaters (Fig. 2), with temporal variability being greatest in the Lower Nechako. Since discharge influences the rate of bottom sediment removal (erosion) and suspended sediment settling (deposition), and causes changes in hydraulic resistance (Manning's n; Vinson *et al.* 1992) and depth, temporal fluctuations in discharge can be interpreted as environmental heterogeneity or perturbation (*sensu* Minshall 1988), such that river reaches with greater fluctuations in discharge (i.e., reaches furthest from headwaters) should be more environmentally heterogenous, at least temporally, than the converse. In this study, the environmental heterogeneity of a reach was defined as the difference between the long-term mean summer (June 15 - August 15) and non-summer (August 16 - June 14) discharge. Thus, environmental heterogeneity in the Nechako River increases with increasing catchment area and has decreased in each of the reaches since the construction of the Kenney Dam (Table 1).

Data analysis

Large scale morphometry (catchment area and longitudinal slope)

Macrophyte species diversity was compared for the Upper, Middle and Lower reaches (i.e., gamma diversity; Whittaker 1972; Vitt *et al.* 1995). Gamma

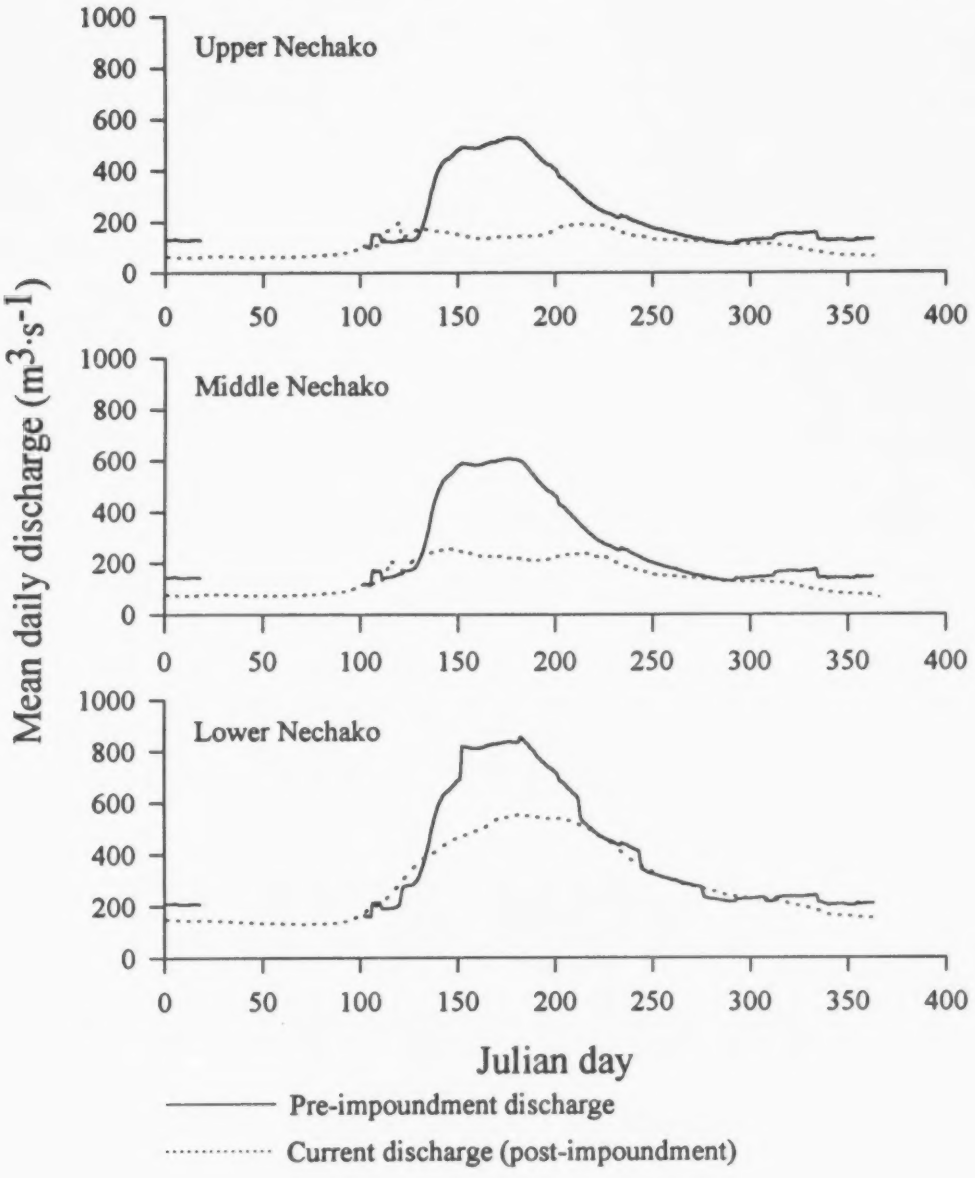

FIGURE 2. Discharge hydrographs ($m^3 \cdot s^{-1}$) for the Upper, Middle and Lower Nechako River, British Columbia, pre and post impoundment (Discharge data supplied by Environment Canada).

TABLE 1. Long-term mean summer (June 15 - August 15) discharge ($m^3 \cdot s^{-1}$) and non-summer (August 16 - June 14) discharge ($m^3 \cdot s^{-1}$) for the Upper, Middle and Lower Nechako River, British Columbia, pre- and post- impoundment (Discharge data from Environment Canada 1991 and shown in Figure 1). Environmental heterogeneity ($m^3 \cdot s^{-1}$) was calculated as the difference between the mean non-summer and mean summer discharge. Catchment area (km^2) post-impoundment includes 14000 km^2 behind the Kenney Dam (after Environment Canada 1991).

River reach	Catchment area (km^2)	Mean summer discharge ($m^3 \cdot s^{-1}$)	Mean non-summer discharge ($m^3 \cdot s^{-1}$)	Environmental heterogeneity ($m^3 \cdot s^{-1}$)
Pre-impoundment				
Lower	42500	699	321	378
Middle	25100	468	221	247
Upper	23730	408	190	218
Post-impoundment				
Lower	42500	525	237	288
Middle	25100	224	129	95
Upper	23730	165	104	61

diversity was expressed as the Shannon-Wiener index (H'; Krebs 1989) and calculated as:

$$H' = \sum_{i=1}^{s} (p_i)(\log_2 p_i) \quad (2)$$

where s is the number of species in the reach and p_i is the proportion of the total biomass in the reach belonging to the *ith* species. Because mosses and macroscopic algae (i.e., *Chara*) were not identified to the level of species, they were not included in calculations of diversity. Percent bottom cover, defined as the distance across the river channel occupied by macrophytes in relation to river width, was determined for each survey site and related to the longitudinal slope of the river and catchment area. As macrophytes were never present at the centre of the channel, percent bottom cover was determined as the sum of the maximum distance that macrophytes occurred from each riverbank and then dividing this value by the mean summer width of the site and multiplying by 100.

Small scale morphometry (near shore cross-sectional slope)

Non-linear regression (Norusis 1993) was used to relate macrophyte biomass to the CSS of the riverbed. Following the approach of Duarte and Kalff (1986), peak biomass (PB), defined as the highest biomass observed at any given slope, was also related to CSS to determine the maximum potential biomass achievable over any given range in slope. CSS's were pooled into intervals of 2.5% (i.e.; 0.0-2.5%, 2.5-5.0%, etc.) and the maximum observed biomass within each grouping was plotted against the centre point of each CSS group. Peak sediment exchangeable N (PSN) and P (PSP) concentrations were also correlated with CSS to see if changes in PB along the CSS gradient tracked changes in sediment nutrients. Using non-linear regression, PB, PSP and PSN were related to CSS with

modified power functions, as in Duarte and Kalff (1986), of the form:

$$y = Ax^{n} + B \quad (3)$$

where y is the dependent variable (PB, PSP or PSN), A is the y-intercept of the fitted line, x is the independent variable (CSS), B is an empirical constant and n is the slope of the fitted line (Spain 1982). The equation variables were estimated iteratively (after Norusis 1993) using non-linear regression for each dependent variable until the lowest possible residual sums of squares was attained. To test for differences in slope between the lines predicting PB, PSP and PSN, an analysis of covariance was performed on log-transformed dependent variables and testing for a significant interaction effect between the dependent variables and near shore cross-sectional slope (*sensu* Norusis 1993).

To investigate the relationship between species diversity and CSS, species diversity (H'; equation 2) was calculated for three CSS categories: (1) low CSS (slopes ≤ 10.0%); (2) moderate CSS (slopes > 10.0 and ≤ 20.0%); (3) high CSS (slopes > 20.0%).

Comparison of Nechako River with the Bow River and Lake Memphremagog

The relationship between CSS and PB in the Nechako River was compared with similar data collected from the Bow River, Alberta, Canada (Alberta Environment upubl. data) and from 43 sites in Lake Memphremagog, Quebec/Vermont, which related PB to the slope of the littoral zone (Duarte and Kalff 1986), to test the hypothesis that near shore slope influences macrophyte biomass in a similar fashion in both lakes and rivers. Since the Lake Memphremagog biomasses were expressed as $g \cdot m^{-2}$ fresh weight, biomasses from Lake Memphremagog were converted to dry weight using a fresh:dry weight ratio of 13.9 (determined from measured fresh and dry weights of 25 macrophyte

samples from the Nechako River). Data for the Bow River were collected by Alberta Environment (unpubl.) using similar methods as to those used on the Nechako River and are described in Chambers *et al.* (1991). As for the Nechako River, slopes for Lake Memphremagog and the Bow River were pooled into intervals of 2.5% (i.e., 0-2.5%, 2.5-5.0% etc.) and related to the peak biomass within each interval.

Results

Macrophytes in the Nechako River

Fourteen macrophyte taxa were found in the Nechako River: *Elodea canadensis* Rich., *Limosella aquatica* L., *Ranunculus aquatilis* L., *Polygonum amphibium* L., *Myriophyllum exalbescens* Fern., *Callitriche hermaphroditica* L., *Ceratophyllum demersum* L., *Sagittaria cuneata* Sheld., *Elatine triandra* Schk., *Potamogeton berchtoldii* Fieb., *Potamogeton gramineus* L., *Potamogeton pectinatus* L., *Potamogeton richardsonii* (Bennett) Rydb., *Chara* and one or more moss species. *E. canadensis* was the dominant species, representing 64% of the total biomass in the river, followed by *P. richardsonii* (12%), *M. exalbescens* (5%), *P. berchtoldii* (5%) and *C. demersum* (3%). The remaining taxa comprised less than 11% of the total macrophyte biomass. Because *L. aquatica*, *P. amphibium* (an emergent species), *S. cuneata* and *E. triandra* were rarely observed, they were excluded from the analysis of species-specific distribution. However, their biomasses were included in analyses of total community biomass and species diversity.

Large scale morphometry (longitudinal slope and catchment area)

Longitudinal slopes of the Upper and Lower Nechako were similar, averaging ~ 0.5 $m \cdot km^{-1}$ (i.e., a 0.5 m change in elevation for every 1 km of river length) (Fig. 3). The Middle Nechako was considerably less steep with a slope of only ~ 0.2 $m \cdot km^{-1}$ (Fig. 3). Sites in the Middle Nechako also had relatively slow channel velocities, averaging 0.6±0.04 $m \cdot s^{-1}$ (mean±1S.E.), while channel velocities at sites in the Upper and Lower Nechako were faster, averaging 1.0±0.04 and 1.6±0.05 $m \cdot s^{-1}$, respectively (Table 2). Since exchangeable N (r = -0.54, P < 0.0001) and P (r = -0.69, P < 0.0001) were found to be negatively correlated with current speed (Fig. 4), the differences in channel velocity observed between reaches suggests that more nutrients may be available to macrophytes in the Middle Nechako than in the Upper and Lower Nechako. The two steeper-sloping reaches had similar (P > 0.05; Tukey-HSD) average bottom cover (2.4±1.3% [n = 9] and 5.6±3.4% [n = 8] for the Upper and Lower Nechako, respectively) while the low gradient Middle Nechako had significantly (P < 0.0001; ANOVA) higher (28±3%; n = 7) bottom cover (Fig. 3; Table 2). While bottom cover was greatest in the low gradient reach, species diversity increased with increasing catchment area, from 0.5 in the Upper Nechako (23730 km^2) to 1.7 and 2.1 in the Middle (25100 km^2) and Lower (42500 km^2) Nechako, respectively (Table 2). As well as differing in species diversity, the three reaches varied with respect to species dominance (Fig. 5). The Lower Nechako was dominated, in terms of biomass, by *P. pectinatus*, mosses and *P. berchtoldii* (Fig. 5). In contrast, the Middle Nechako was dominated by *E. canadensis*, *P. richardsonii* and *M. exalbescens* and the Upper Nechako by *E. canadensis*, *P. richardsonii* and *R. aquatilis* (Fig. 5). The growth-form structure of the dominant species was similar for the Upper and Middle Nechako, both being dominated by a highly dissected species (*E. canadensis*), a broad-leafed species (*P. richardsonii*) and a needle-leafed species (i.e., *M. exalbescens* in the Middle

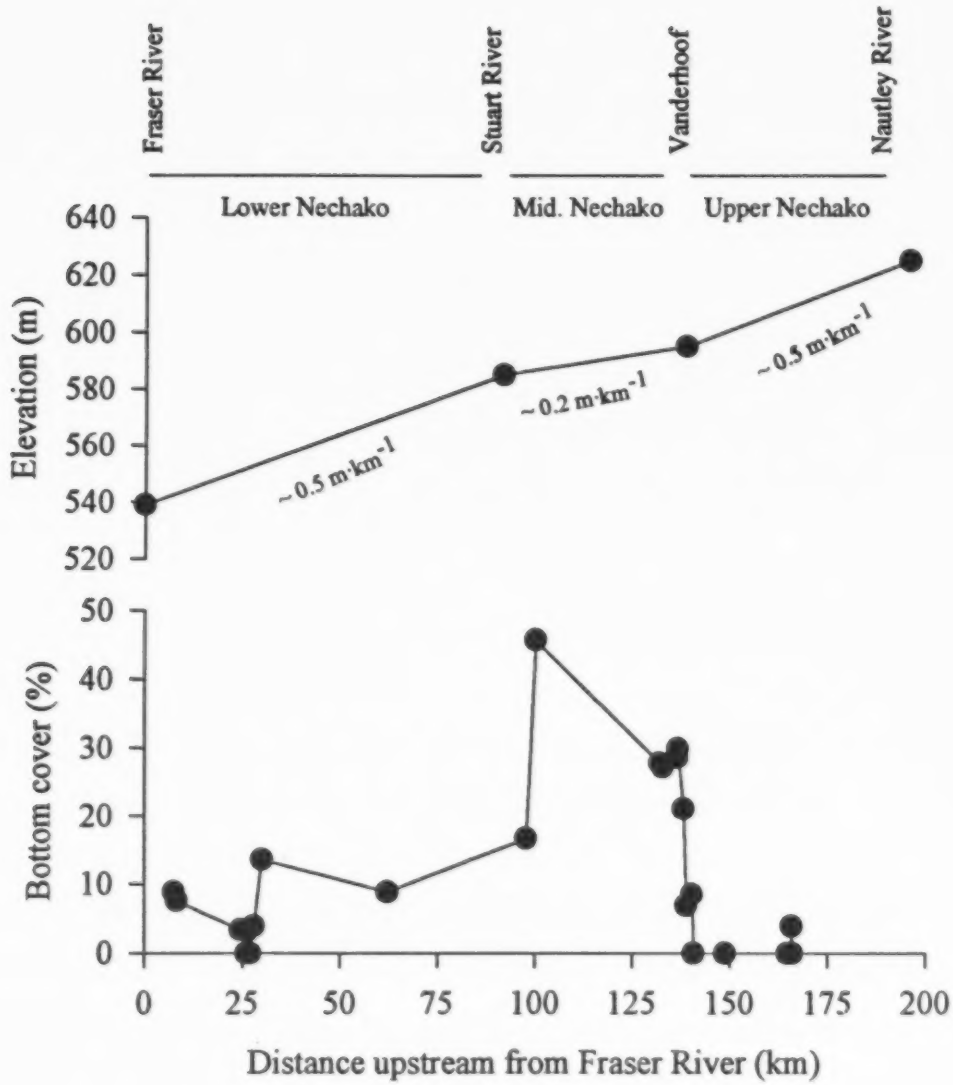

FIGURE 3. Macrophytic bottom cover (%) in the Nechako River in relation to longitudinal slope (%). NOTE: only 24 sites shown on lower panel because longitudinal slope was not determined for two sites upstream of the Nautley River inflow.

TABLE 2. Longitudinal slope ($m \cdot km^{-1}$), mean summer channel speed ($m \cdot s^{-1}$), mean macrophytic bottom cover (%, mean±1S.E.) and species diversity (gamma; H') of three reaches of the Nechako River, British Columbia. (Summer channel velocity data from French and Chambers (in prep.)). NOTE: only vascular plants used in calculations of gamma diversity.

River reach	Longitudinal slope ($m \cdot km^{-1}$)	Mean summer channel speed ($m \cdot s^{-1}$ ± 1 S.E.)	Mean bottom cover (% ± 1 S.E.)	H' (Shannon-Wiener index of diversity)
Upper	0.5	1.0 ± 0.04	2.4 ± 1.3 (n = 9)	0.5
Middle	0.2	0.6 ± 0.04	28.1 ± 3.4 (n = 7)	1.7
Lower	0.5	1.6 ± 0.05	5.6 ± 3.4 (n = 8)	2.1

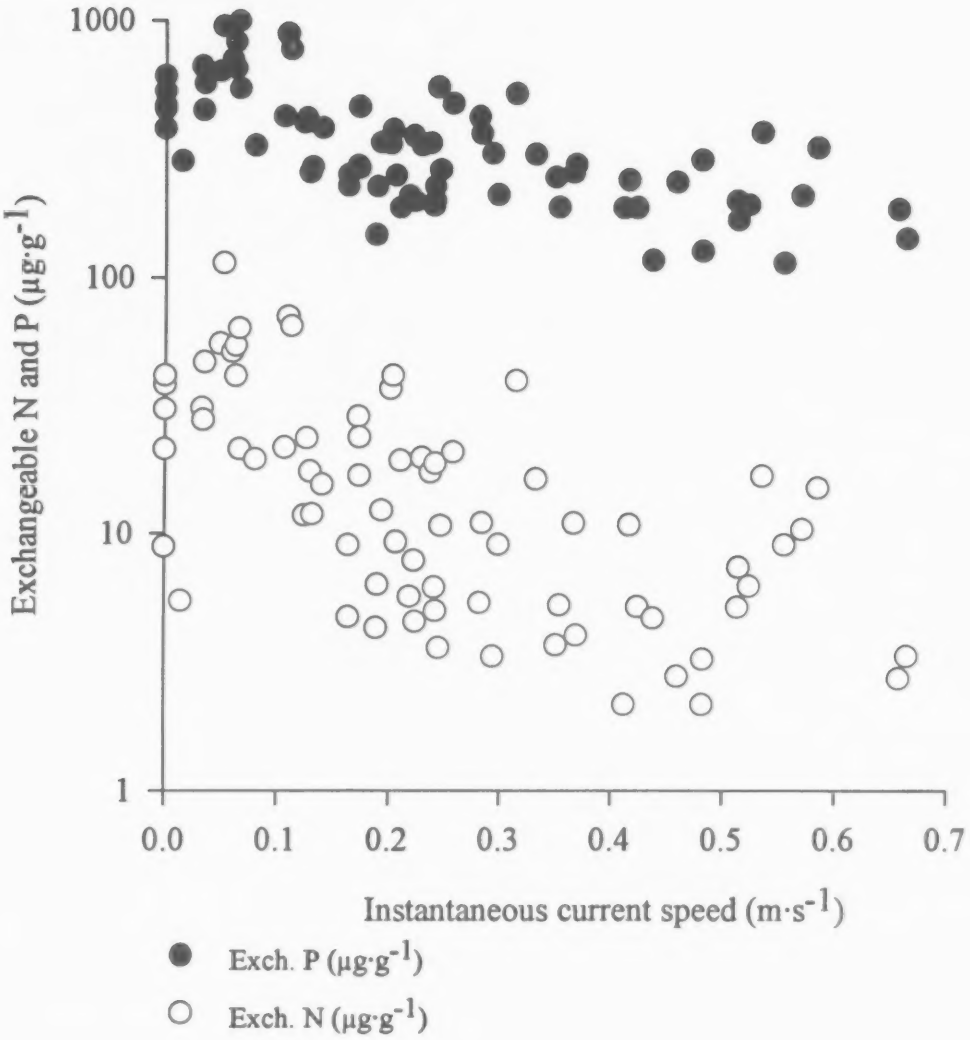

FIGURE 4. Sediment exchangeable nitrogen and phosphorus concentrations ($\mu g \cdot g^{-1}$ dry weight) in relation to current speed ($m \cdot s^{-1}$) for the Nechako River, British Columbia.

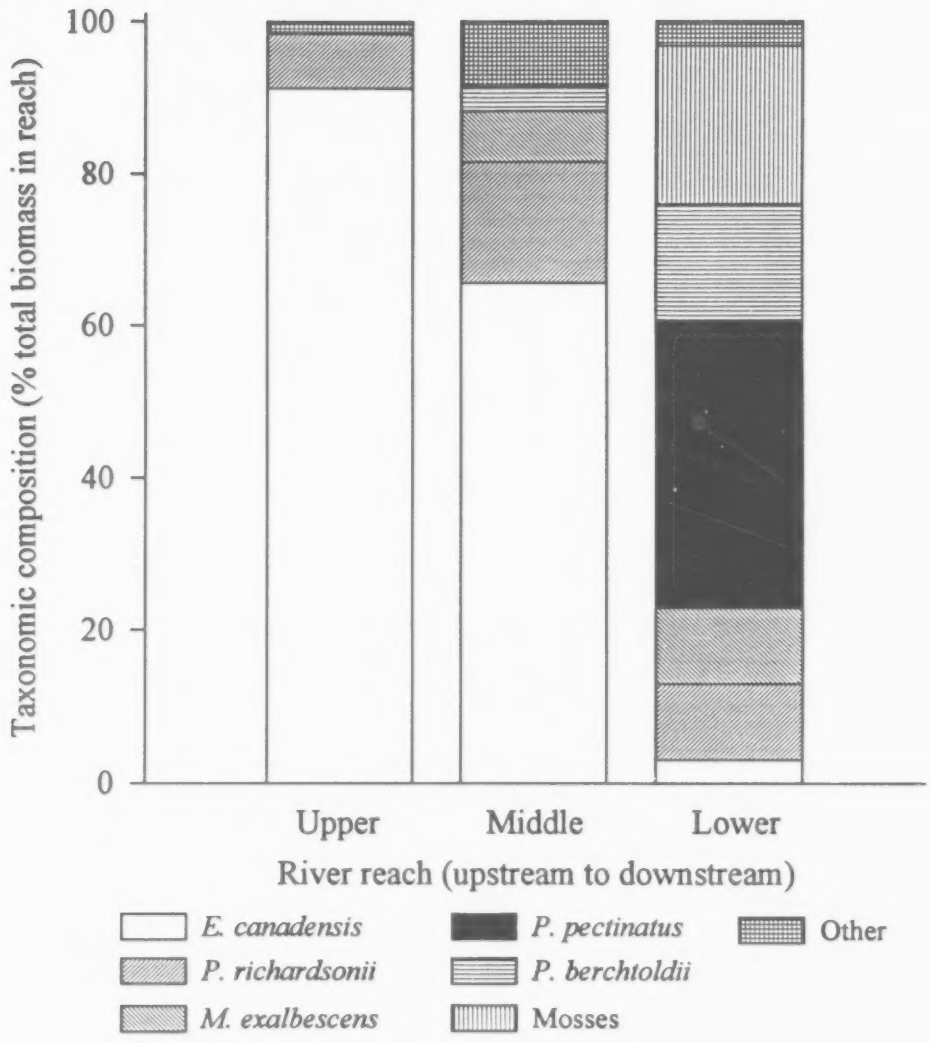

FIGURE 5. Taxonomic composition (% total biomass in reach) in the Upper, Middle and Lower Nechako River.

Nechako and *R. aquatilis* in the Upper Nechako). In contrast, the Lower Nechako was dominated by two fine-leafed species (i.e., *P. pectinatus* and *P. berchtoldii*) and mosses which have a cushion-like growth-form.

Small scale morphometry (near shore cross-sectional slope)

CSS in the Nechako River ranged from 0 to 40%. Macrophyte biomass was more variable in regions of low (≤ 10%) than high (> 10%) CSS (Fig. 6), ranging from 0 to 1262 $g \cdot m^{-2}$ (154±32 $g \cdot m^{-2}$; n = 85) for slopes ≤ 10% as compared to 0 to 582 $g \cdot m^{-2}$ (78±17 $g \cdot m^{-2}$; n = 45) for slopes > 10%. There was, however, no significant difference (P = 0.41; Mann-Whitney U test) in biomass between low and high slope regions due to large variations in biomass within each slope interval (Fig. 6).

While biomass was not correlated with CSS when all data were considered, PB decreased with increasing CSS such that PB was 1262 and 34 $g \cdot m^{-2}$ in the lowest (0.0-2.5%) and the highest (37.5-40.0%) CSS regions, respectively (Fig. 7). The equation predicting PB from slope is

$$PB = -44577 + 46071CSS^{-0.009} \quad (4)$$

$r^2 = 0.78$, $n = 16$, $F = 32.7$ ($P < 0.001$), $SE_A = 1389849$, $SE_n = 0.28$, $SE_B = 1390031$ where PB is peak biomass ($g \cdot m^{-2}$ dry weight) for a given slope interval and CSS is the cross-sectional slope (%) of the riverbed.

PSP and PSN also decreased with increasing CSS (Fig. 8). PSP was 949 and 424 $\mu g \cdot g^{-1}$ dry weight at CSS's of 0.0-2.5% and 37.5-40.0%, respectively, while PSN was 114 and 15 $\mu g \cdot g^{-1}$ dry weight over the same CSS intervals (Fig. 8). The equations predicting PSP and PSN from CSS were:

$$PSP = -1568 + 2648CSS^{-0.098} \quad (5)$$

$r^2 = 0.68$, $n = 16$, $F = 63.7$ ($P < 0.001$), $SE_A = 7597$, $SE_n = 0.30$, $SE_B = 7714$

$$PSN = -4.0 + 134CSS^{-0.51} \quad (6)$$

$r^2 = 0.77$, $n = 16$, $F = 43.1$ ($P < 0.001$), $SE_A = 25$, $SE_n = 0.30$, $SE_B = 30$

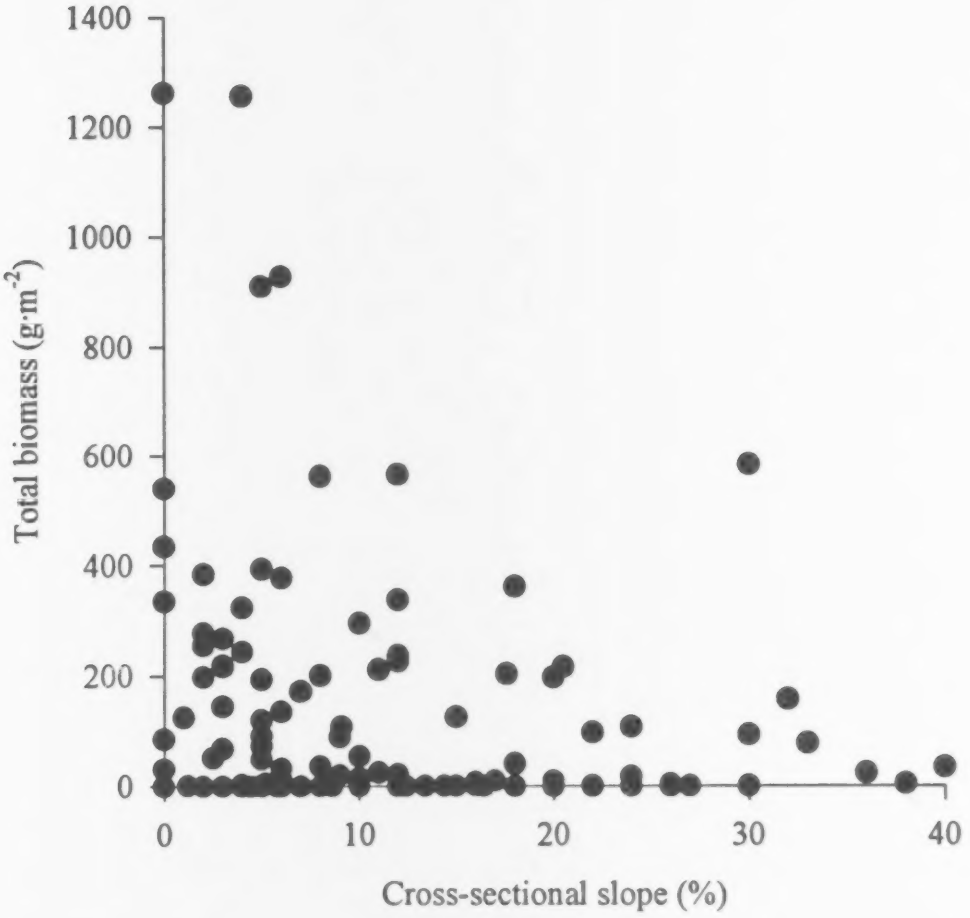

FIGURE 6. Relationship between submerged macrophyte biomass ($g \cdot m^{-2}$ dry weight) and near shore cross-sectional slope (%) for the Nechako River, British Columbia.

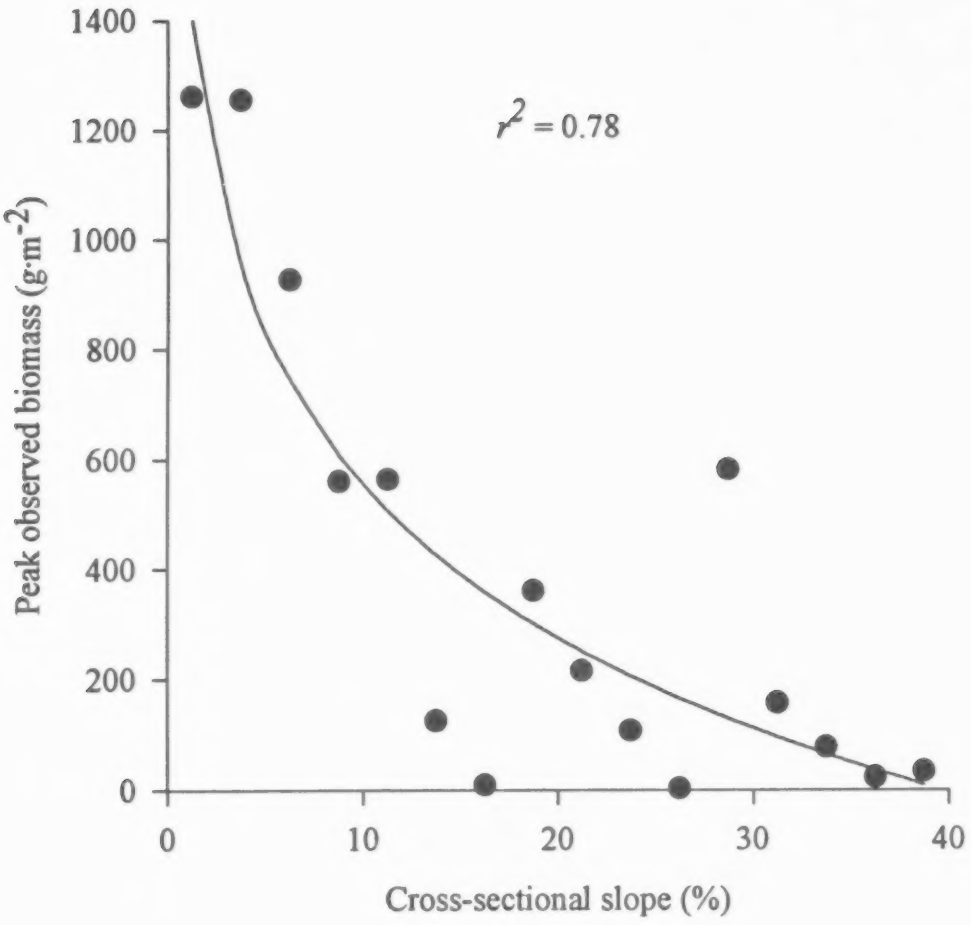

FIGURE 7. Peak submerged macrophyte biomass ($g \cdot m^{-2}$ dry weight) in relation to near shore cross-sectional slope (%) for the Nechako River, British Columbia.

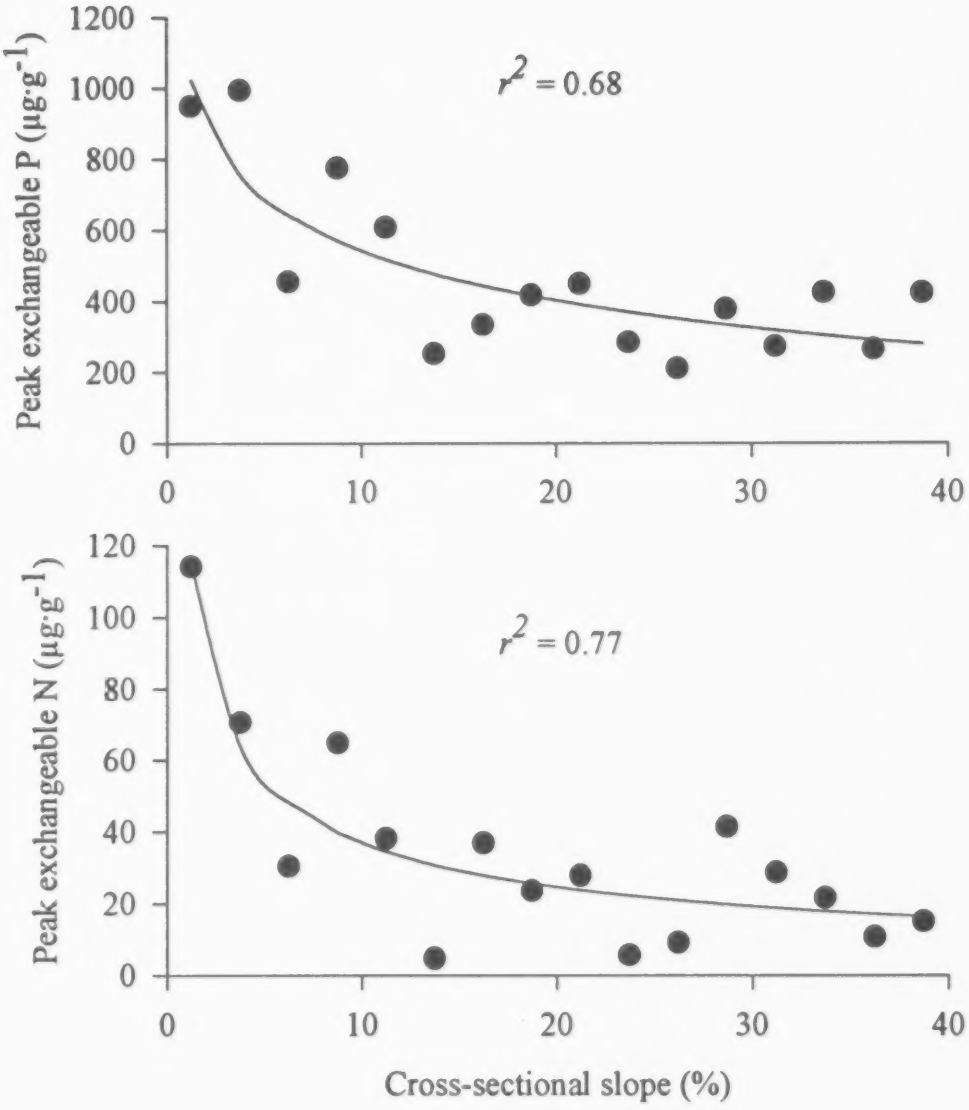

FIGURE 8. Peak sediment exchangeable phosphorus and nitrogen concentrations ($\mu g \cdot g^{-1}$ dry weight) in relation to near shore cross-sectional slope (%) for the Nechako River, British Columbia.

where PSP is peak sediment exchangeable phosphorus concentration ($\mu g \cdot g^{-1}$) for a given slope interval, PSN is peak sediment exchangeable nitrogen ($\mu g \cdot g^{-1}$) for a given slope interval and CSS is the cross-sectional slope (%) of the riverbed.

While PB of the macrophyte community decreased ($P < 0.001$) with increasing CSS, species differed in their distribution with respect to CSS. Thus, PB of *E. canadensis* decreased sharply with increasing slope over the range 0.0-27.5% (Fig. 9). Other species attained their greatest biomasses in regions of high (20.0-22.5%) (e.g., *R. aquatilis*) or moderate (5.0-10.0%) CSS (e.g., *C. demersum*, *C. hermaphroditica*, *P. pectinatus*, *M. exalbescens* and *Chara*) (Fig. 9). However, some species (e.g., *P. gramineus* and *P. richardsonii*) showed no clear relationship with CSS, being abundant at a wide range of CSS's (Fig. 9). In terms of frequency of occurrence (expressed as the ratio of the number of occurrences to the total number of plots × 100), *C. demersum* occurred most frequently at slopes of 0.0-2.5%, whereas *P. gramineus*, *P. pectinatus*, *Potamogeton berchtoldii*, mosses and *R. aquatilis* were most frequently observed at slopes greater than 30% (Fig. 10). *C. hermaphroditica* occurred most frequently at moderately high slopes (12.5-15.0%), while *E. canadensis*, *M. exalbescens*, *P. richardsonii* and *Chara* occurred sporadically over the entire CSS gradient (Fig. 10). Species diversity was lower at CSS's ≤ 10.0% (H' = 1.6) than at moderate (10.0 - ≤ 20.0%) and steep (> 20.0%) slopes where H' was 2.0 and 1.9, respectively.

Comparison of Nechako River with the Bow River and Lake Memphremagog

The macrophyte community of Lake Memphremagog consisted of 15 taxa (Chambers 1987), a comparable number to that found in the Nechako River (i.e., 14). Of these, five taxa were in common to the Nechako River: *C. demersum*, *E. canadensis*, *P. gramineus*, *P. richardsonii* and *Chara*. By comparison, the macrophyte community of the Bow River was less diverse, with only four species

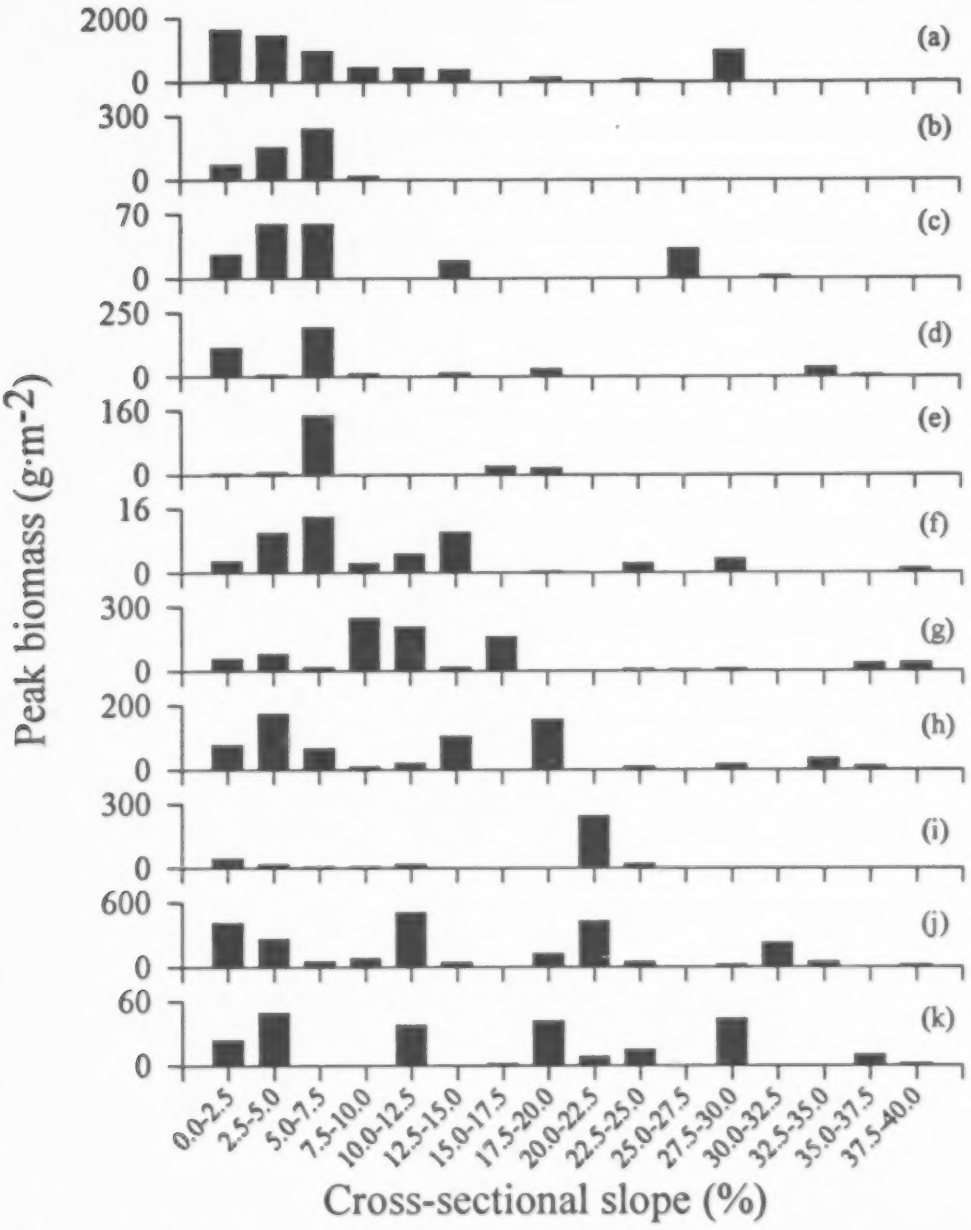

FIGURE 9. Peak biomass ($g \cdot m^{-2}$ dry weight) of submerged macrophyte species in relation to near shore cross-sectional slope (%) as observed for the Nechako River, British Columbia. (a) *Elodea canadensis*, (b) *Ceratophyllum demersum*, (c) *Callitriche hermaphroditica*, (d) *Potamogeton pectinatus*, (e) mosses, (f) *Chara*, (g) *Myriophyllum exalbescens*, (h) *Potamogeton berchtoldii*, (i) *Ranunculus aquatilis*, (j) *Potamogeton richardsonii* and (k) *Potamogeton gramineus*.

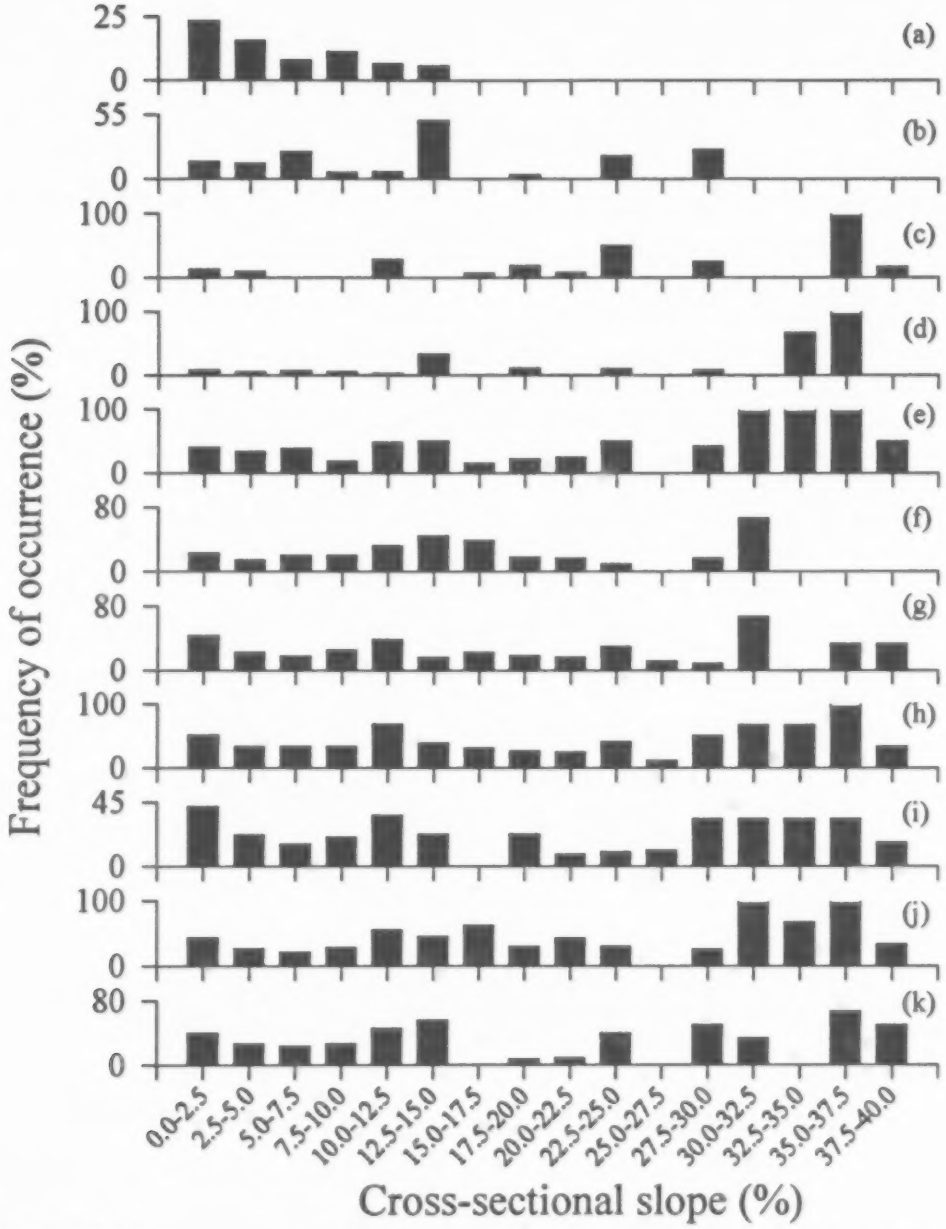

FIGURE 10. Frequency of occurrence (%) of submerged macrophyte species in relation to near shore cross-sectional slope (%) for the Nechako River, British Columbia. (a) *Ceratophyllum demersum*, (b) *Callitriche hermaphroditica*, (c) *Potamogeton gramineus*, (d) *Potamogeton pectinatus*, (e) *Potamogeton berchtoldii*, (f) mosses, (g) *Ranunculus aquatilis*, (h) *Elodea canadensis*, (i) *Myriophyllum exalbescens*, (j) *Potamogeton richardsonii* and (k) *Chara*.

predominating (*Potamogeton vaginatus*, *Potamogeton crispus*, *P. pectinatus* and *Zannichellia palustris*; Charlton *et al.* 1986), only one of which was common to the Nechako River (i.e., *P. pectinatus*). Growth-form composition of the macrophyte community was also similar for both the Nechako River and Lake Memphremagog in that both had canopy-producing (e.g., *C. demersum*, *M. exalbescens* and *M. spicatum*), erect (e.g., *E. canadensis*, *P. gramineus* and *P. richardsonii*) and bottom-dwelling (e.g., *Chara* and *L. triandra*) forms. In contrast, the growth-form structure of the Bow River's macrophyte community was less complex, with all taxa being erect forms.

As in the Nechako River, PB was negatively correlated with near-shore slope in Lake Memphremagog (Fig. 11). However, biomasses were lower in Lake Memphremagog for any given slope interval. Thus, PB in Lake Memphremagog was 195 $g \cdot m^{-2}$ at low slope sites (0.0-2.5%) and 3 $g \cdot m^{-2}$ at high slope sites (27.5-30.0%) as compared to 1262 and 582 $g \cdot m^{-2}$ for similar slope intervals in the Nechako River (Fig. 11). In contrast, the curvilinear decrease in PB with increasing CSS for the Nechako River and Lake Memphremagog was not observed in the Bow River ($P > 0.05$). However, PB in the Bow River was greater in regions of low (< 10%) than high (> 10%) CSS ($P = 0.01$; Mann-Whitney U).

Discussion

Bottom cover and structure (i.e., species diversity and dominance) of riverine macrophyte communities were found to be correlated with catchment area and longitudinal slope. Thus, macrophytic bottom cover in the Nechako River was greater in areas of low (~ 0.2 $m \cdot km^{-1}$) than high (~ 0.5 $m \cdot km^{-1}$) longitudinal slope, averaging 2.4±1.3% and 5.6±3.4% in high gradient reaches (Upper and Lower Nechako, respectively) compared to 28.1±3.4% in the low gradient reach

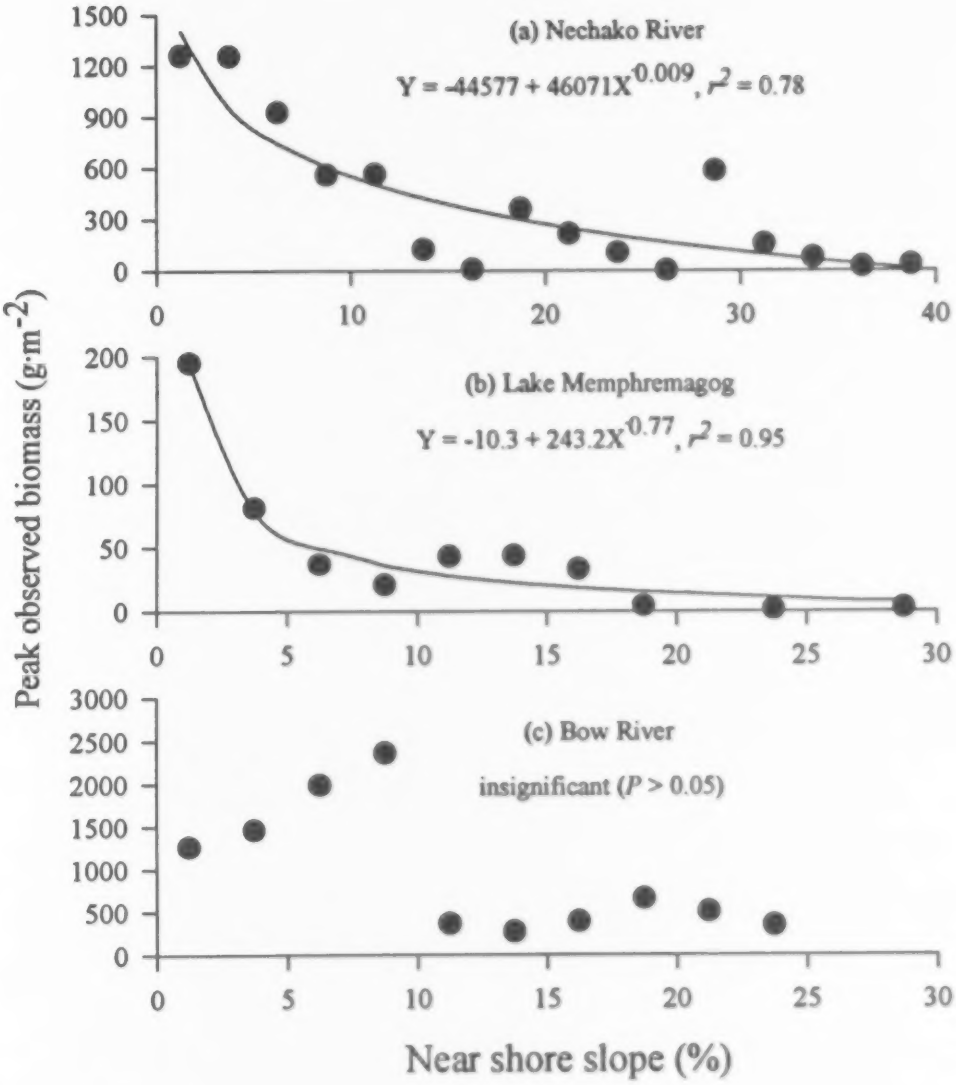
(a) Nechako River
Y = -44577 + 46071X^-0.009, r^2 = 0.78
(b) Lake Memphremagog
Y = -10.3 + 243.2X^-0.77, r^2 = 0.95
(c) Bow River
insignificant (P > 0.05)
Peak observed biomass (g·m-2)
Near shore slope (%)

FIGURE 11. Peak submerged macrophyte biomass ($g \cdot m^{-2}$ dry weight) in relation to near shore slope (%) for the Nechako River, British Columbia, Lake Memphremagog, Quebec/Vermont and Bow River, Alberta (note differences in y-axis scale).

(Middle Nechako). Longitudinal slope likely affects macrophyte abundance indirectly by affecting channel velocity, since high gradient reaches had faster channel velocities than the low gradient reach (Table 2). This hypothesis is consistent with other studies which have shown that the growth of macrophytes is facilitated by slow current velocities. For example, Chambers *et al.* (1991) found that macrophyte biomass was significantly ($P < 0.0005$) and inversely correlated ($r > -0.68$) with current velocity over the range 0.01-1 $m \cdot s^{-1}$ in the Bow River. Furthermore, Chambers *et al.* (1991), using an *in situ* experimental approach, showed that the growth rate of *P. pectinatus* decreased with increasing current velocity over the range 0.2 - 0.7 $m \cdot s^{-1}$, irrespective of changes in sediment nutrient content. Since the exchangeable N and P content of the bottom sediments were negatively correlated with current speed (Fig. 4) and riverine macrophytes obtain most of their nutrients from the bottom sediments (Chambers *et al.* 1989), the low gradient reach would have also had more nutrients available for macrophyte growth.

The observation that gamma diversity (H') increased along the length of the Nechako River (from 0.5, 1.7, to 2.1 for the Upper, Middle and Lower Nechako, respectively (Table 2)) is consistent with longitudinal changes in invertebrate and fish communities reported for other rivers. For example, Minshall *et al.* (1985b), showed that species richness of benthic invertebrate communities increases with increasing distance from the headwaters in small to medium sized streams. Similarly, Minshall (1988) and Statzner and Higler (1985) hypothesized that species diversity is often greatest in the lower reaches of rivers due to their greater physical heterogeneity. In this paper it is suggested that the observed downstream increase in macrophyte diversity is attributable to the greater variability in discharge in the downstream reaches; where discharge variability is a function of catchment area (Table 1). In agreement with this hypothesis, the "river continuum concept" (Vannote *et al.* 1980) theorizes that total community diversity is greatest

in river reaches having high degrees of physical variability. The findings of this study also conform to the intermediate disturbance hypothesis (Connell 1978; Ward and Stanford 1983) which postulates that biodiversity is greatest in habitats with intermediate levels of disturbance as compared with habitats with low levels and extremely high levels of disturbance; thus, in view of the Nechako River, the Upper and Middle reaches may be low-disturbance reaches, whereas the Lower reach may experience a more intermediate degree of disturbance in terms of discharge fluctuations. As do Vannote *et al.* (1980) and Minshall (1988) we suggest that discharge fluctuation is a satisfactory measure of environmental heterogeneity and disturbance since discharge affects several physical attributes of the riverine environment, including the rate of bottom sediment removal and suspended sediment settling, hydraulic resistance (Vinson *et al.* 1992) and depth.

In addition to differences in species diversity, the three reaches of the Nechako River also varied in species dominance with the Lower Nechako being dominated by *P. pectinatus*, mosses and *P. berchtoldii*, the Middle by *E. canadensis*, *P. richardsonii* and *M. exalbescens* and the Upper by *E. canadensis*, *P. richardsonii* and *R. aquatilis* (Fig. 5). According to Greenslade (1983), *P. pectinatus*, mosses and *P. berchtoldii* would be classed as r-strategists since they are adapted to unstable environments, while *E. canadensis*, *P. richardsonii*, *M. exalbescens* and *R. aquatilis* would be k-strategists since they dominated reaches with stable habitats. While the results showed that macrophyte species diversity and bottom cover are related to large scale changes in river morphometry (i.e, catchment area and longitudinal slope), riverine macrophyte communities were also found to be affected by small scale morphometry. Thus, submerged macrophyte biomass in the Nechako River was greater in regions of low than high CSS (Fig. 7). These results are consistent with those from lake studies (e.g., Duarte and Kalff 1986; Duarte *et al.* 1986) which have shown that the peak biomass of submerged

and emergent macrophyte communities is negatively correlated with the slope of the littoral zone (Fig. 11). Rooted aquatic macrophytes obtain most of their nutrients from the bottom sediments (e.g., Welsh and Denny 1979; Barko and Smart 1980; Carignan and Kalff 1980; Barko and Smart 1981; Chambers *et al.* 1989). The observation that peak sediment exchangeable N and P were negatively correlated with CSS (Figs. 6 & 7) suggests that CSS influences the distribution of aquatic macrophytes indirectly by affecting the nutrient content of bottom sediments. This mechanism is consistent with Hakanson (1977) who reported that fine sediments, which are usually more nutrient rich than coarse sediments, are lost from steep slopes through erosional processes, whereas gradual slopes tend to accumulate fine sediments through depositional processes. In addition to slope affecting the nutrient content of riverbed sediments, the movement of sediments on steep slopes may disturb the rooting structures of macrophytes, thus hindering their growth and colonization (Pearsall 1917; Petts 1984; Duarte and Kalff 1986). While PB and CSS showed a curvilinear relationship for the Nechako River and Lake Memphremagog, there was no such relationship between PB and CSS for the Bow River ($P > 0.05$; Fig. 11). However, macrophyte biomass in the Bow River was greater in regions of low (< 10%) CSS than high (> 10%) CSS ($P = 0.01$). The observations that macrophyte species differ in their habitat use with respect to CSS (Figs. 9 & 10) and that macrophyte species composition was similar for the Nechako River and Lake Memphremagog but very different for the Bow River suggests that differences in macrophyte community species composition may explain the inverse curvilinear relationship between PB and CSS for the Nechako River and Lake Memphremagog and the lack of a similar relationship for the Bow River. While PB was greater in regions of low near-shore slope than in regions of high near-shore in the Nechako River, Bow River and Lake Memphremagog, biomasses in Lake Memphremagog were comparatively low such that biomasses were often greater than 600 $g \cdot m^{-2}$ in the Nechako and Bow rivers whereas biomass

peaked at about 200 $g \cdot m^{-2}$ in Lake Memphremagog (Fig. 11). Nutrient chemistry data available for two sub-basins in Lake Memphremagog (Anderson and Kalff 1986 a,b) indicate that sediment exchangeable P ranges from about 26 to 168 $\mu g \cdot g^{-1}$ in Lake Memphremagog's littoral zone. In comparison, sediment exchangeable P was much greater in the Nechako River (114 - 993 $\mu g \cdot g^{-1}$) and Bow River (163 - 609 $\mu g \cdot g^{-1}$, samples taken from sites downstream of the City of Calgary's, AB, sewage treatment plant and analyzed as "biologically available P"; Cross *et al.* 1986). Thus, the observation that the Nechako and Bow rivers had greater biomass than Lake Memphremagog over any given slope interval (Fig. 11) may be attributable to the relatively low nutrient content of Lake Memphremagog's bottom sediments.

In conclusion, the results of this study showed that macrophyte community structure in rivers is related to both large and small scale morphometric variables. On a large scale, abundance and species diversity were related to longitudinal slope and catchment area (which is positively correlated with environmental heterogeneity), respectively, while, on a smaller scale, peak biomass was correlated with near shore cross-sectional slope. While data presented in Chapter II of this thesis indicates that the distribution and abundance of submerged aquatic macrophytes is largely a function of current velocity, it is likely that morphometry exerts ultimate control over riverine macrophyte communities since current velocity in river channels is largely determined by channel geometry (Hogan and Church 1989; Bras 1990; Gordon *et al.* 1992) and discharge (Chapter 2 - Fig. 3 of this thesis; Gray 1970), where discharge is a function of catchment area. The results of this study are important when considering the impacts of river impoundment on biodiversity and that the preservation of biodiversity is one of the key issues in contemporary ecology (Government of Canada 1990; Hunter 1990; Kaufman and Franz 1993; Raven *et al.* 1993). While studies on man's impacts on biodiversity have largely focused on species diversity in tropical rainforests (Raven *et al.* 1993),

few studies have investigated the potential effects of river impoundment on the biodiversity of lotic ecosystems. Data presented in this study indicate that impoundment can reduce the environmental heterogeneity of a river by decreasing temporal discharge variability (Table 1). Thus, the finding that the diversity of macrophyte communities in the Nechako River is positively correlated with environmental heterogeneity suggests that river impoundment may reduce the diversity of riverine macrophyte communities and favoured species which are k-strategists (e.g., *E. canadensis*). Since aquatic macrophytes serve as food and habitat for other organisms (e.g., invertebrates and fishes), river impoundment could, in turn, result in a reduction in diversity in other trophic levels (e.g. aquatic animals). This hypothesis is reasonable if one views aquatic "forests" to be comparable to terrestrial forests in which structural complexity (derived from plant species diversity) is positively correlated with animal (e.g., birds) diversity (MaCarthur 1964; Rickleffs 1977). This hypothesis is further supported by *in situ* ecological studies in temperate marine environments which have shown that the structural complexity of kelp forests, where complexity is derived from diversity in macroalgal growth-form (e.g., floating, stipate, prostrate, turf and pavement forms; Dayton and Tegner 1984), is associated with diverse invertebrate and fish communities, whereas marine environments without kelp forests often have relatively less diverse animal communities (Nybakken 1993). Further research on the ecological significance of macrophyte species diversity in aquatic ecosystems is required to better understand the implications of losses in macrophyte diversity.

References Cited

ANDERSON, M. R., AND J. KALFF. 1986a. Regulation of submerged aquatic plant distribution in a uniform area of a weedbed. J. Ecol. **74:** 953-961.

ANDERSON, M. R., AND J. KALFF. 1986b. Nutrient limitation of *Myriophyllum spicatum* growth in situ. Freshwater Biol. **16:** 735-743.

BARKO, J. W., AND R. M. SMART. 1980. Mobilization of sediment phosphorus by submersed freshwater macrophytes. Freshwater Biol. **10:** 229-238.

BARKO, J. W., AND R. M. SMART. 1981. Sediment-based nutrition of submersed macrophytes. Aquat. Bot. **10:** 339-352.

BOTHWELL, M. L. 1992. Eutrophication of rivers by nutrients in treated kraft pulp mill effluent. Water Pollut. Res. Can. **27:** 447-472.

BRAS, R. L. 1990. Hydrology, an introduction to hydrologic science. Addison-Wesley Publishing Company, New York. 643 pp.

BREMNER, J. M. 1965. Inorganic forms of nitrogen, p. 1179-1237. *In*, C. A. Black [Ed.] Methods of Soil Analysis. American Society of Agronomy; Inc., Madison, WI. 1572 p.

BRITISH COLUMBIA DEPARTMENT OF ENERGEY, MINES AND RESOURCES. 1977. Surveys and Mapping Branch. 1:50000 Maps, British Columbia.

CARPENTER, S. R. 1983. Lake geometry: implications for production and sediment accretion rates. J. Theor. Biol. **105:** 273-286.

CARIGNAN, R., AND J. KALFF. 1980. Phosphorus sources for aquatic weeds: water or sediments? Science **207:** 987-989.

CASTENHOLZ, R. W. 1969. Thermophilic blue-green algae and the thermal environment. Bacteriol. Rev. **33:** 476-504.

CHAMBERS, P. A. 1987. Light and nutrients in the control of aquatic plant community structure. II. *In situ* observations. J. Ecol. **75:** 621-628.

CHAMBERS, P. A., AND E. E. PREPAS. 1988. Underwater spectral attenuation and its effect on the maximum depth of angiosperm colonization. Can. J. Fish. Aquat. Sci. **45:** 1010-1017.

CHAMBERS, P. A., E. E. PREPAS, M. L. BOTHWELL, AND H. R. HAMILTON. 1989.

Roots versus shoots in nutrient uptake by aquatic macrophytes in flowing waters. Can. J. Fish. Aquat. Sci. **46:** 435-439.

CHAMBERS, P. A., E. E. PREPAS, H. R. HAMILTON, AND M. L. BOTHWELL. 1991. Current velocity and its effect on aquatic macrophytes in flowing waters. Ecol. Appl. **1:** 249-257.

CHARLTON, S. E. D., H. R. HAMILTON, AND P. M. CROSS. 1986. The limnological characteristics of the Bow, Oldman, and South Saskatchewan Rivers (1979 - 1982). Part II. The primary producers. Alberta Environment Water Quality Control Branch, Edmonton, Alberta, Canada.

CONNELL, J. H. 1978. Diversity in tropical rainforests and coral reefs. Science **199:** 1302-1310.

CROSS, P. M., H. R. HAMILTON, AND S. E. D. CHARLTON. 1986. The Limnological Characteristics of the Bow, Oldman and South Saskatchewan Rivers, Part I. Nutrient and Water Chemistry. Alberta Environment, Pollution Control Division, Edmonton, Alberta.

DAYTON, P. K., AND M. J. TEGNER. 1984. The importance of scale in community ecology: a kelp forest example with terrestrial analogs. *In*, Price, P. W., C. N. Slobodchikoff, and W. S. Gaud [Eds.]. 1984. John Wiley & Sons, Inc., New York. p. 457-481.

DILLON, P. J., AND F. H. RIGLER. 1974. A test of a simple nutrient budget model predicting the phosphorus concentration in lake water. J. Fish. Res. Board Can. **11:** 1771-1778.

DUARTE, C. M., AND J. KALFF. 1986. Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. Limnol. Oceanogr. **31:** 1072-1080.

DUARTE, C. M., J. KALFF, AND R. H. PETERS. 1986. Patterns in biomass and cover of aquatic macrophytes in lakes. Can. J. Fish. Aquat. Sci. **43:** 1900-1908.

ENGSTROM, D. R. 1987. Influence of vegetation and hydrology on the humus budgets of Labrador lakes. Can. J. Fish. Aquat. Sci. **44:** 1306-1314.

ENVIRONMENT CANADA. 1991. Historical streamflow summary, British Columbia, to 1990. Environment Canada, Inland Waters Directorate, Water Resources Branch, Water Survey of Canada, Ottawa, Canada.

FEE, E. J. 1979. A relationship between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments. Limnol. Oceanogr. **24:** 401-416.

GORDON, N. D., T. A. MCMAHON, AND B. L. FINLAYSON. 1992. Stream hydrology, an introduction for ecologists. John Wiley & Sons, Inc., Toronto. 526 pp.

GORHAM, E., W. E. DEAN, AND J. E. SANGER. 1983. The chemical composition of lakes in the north-central United States. Limnol. Oceanogr. **28:** 287-301.

GORHAM, E., J. K. UNDERWOOD, F. B. MARTIN, AND J. G. OGDEN III. 1986. Natural and anthropogenic causes of lake acidification in Nova Scotia. Nature **324:** 451-453.

GOVERNMENT OF CANADA. 1990. Canada's green plan. Minister of Supply and Services Canada, 1990, Printing Services, Canada Communications Group. 174 pp.

GRAY, D. M. 1970. Handbook on the principles of hydrology: A general text with special emphasis on Canadian conditions. Secratariat, Canadian National Committee for the International Hydrologic Decade.

GREENSLADE, P. J. M. 1983. Adversity selection and the habitat template. Am. Nat. **122:** 352 -365.

HAAG, R. W., AND P. R. GORHAM. 1977. Effects of thermal effluent on standing crop and net production of *Elodea canadensis* and other submerged macrophytes in Lake Wabamun, Alberta. J. Appl. Ecol. **14:** 835-851.

HAKANSON, L. 1977. The influence of wind, fetch and water depth on the

distribution of sediments in Lake Vanern, Sweden. Can. J. Earth Sci. **14:** 397-412.

HOGAN, D. L., AND M. CHURCH. 1989. Hydraulic geometry in small, coastal streams: progress towards quantification of salmonid habitat. Can. J. Fish. Aquat. Sci. **46:** 844-852.

HUNTER, M. J., JR. 1990. Wildlife, forests, and forestry, principles of managing forests for biological diversity. Prentic Hall, Englewood Cliffs, N. J. 370 pp.

HYNES, H. B. N. 1970. The ecology of running waters. Liverpool University Press, Liverpool.

KAUFMAN, D. G., AND C. M. FRANZ. 1993. Biosphere 2000, protecting our global environment. HarperCollins College Publishers, NY. 607 pp.

KERR, S. R. AND R. A. RYDER. 1988. The applicability of fish yield indices in freshwater and marine ecosystems. Limnol. Oceanogr. **33:** 973-981.

KIRCHNER, W. B., AND P. J. DILLON. 1975. An empirical method of estimating the retention of phosphorus in lakes. Water Res. R. **31:** 182-183.

KREBS, C. J. 1989. Ecological methodology. Harper Collins Publishers, New York, NY. 654 pp.

LARKIN, P. A. 1964. Canadian lakes. Verh. Int. Ver. Theor. Angew. Limnol. **15:** 76-90.

MACARTHUR, R. H. 1964. Environmental factors affecting bird species diversity. Am. Nat. **98:** 387-397.

MATUSZEK, J. E. 1978. Empirical predictions of fish yields of large North American lakes. Trans. Am. Fish. Soc. **107:** 385-394.

MINSHALL, G. W., K. W. CUMMINS, R. C. PETERSEN, C. E. CUSHING, D. A. BRUNS, J. R. SEDELL, AND R. L. VANNOTE. 1985a. Developments in stream ecosystem theory. Can. J. Fish. Aquat. Sci. **42:** 1045-1055.

MINSHALL, G. W., R. C. PETERSEN, JR., AND C. F. NIMZ. 1985b. Species richness in streams of different size from the same drainage basin. Am. Nat. **125:** 16-38.

MINSHALL, G. W. 1988. Stream ecosystem theory: a global perspective. J. North Am. Benthol. Soc. **7:** 263-288.

MOORE, J. E., AND R. J. LOVE. 1977. Effect of pulp and paper mill effluent on the productivity of periphyton and phytoplankton. J. Fish. Res. Board Can. **34:** 856-862.

MURPHY, J. A., J. L. RILEY. 1962. A modified single solution method for the determination of inorganic phosphate in natural waters. Anal. Chim. Acta **27:** 31-36.

NILSSON, C. 1987. Distribution of stream-edge vegetation along a gradient of current velocity. J. Ecol. **75:** 513-522.

NORUSIS, M. J. 1993. SPSS for Windows, advanced statistics. SPSS Inc. 578 pp.

NYBAKKEN, J. W. 1993. Marine biology, an ecological approach (3rd edition). HarperCollins College Publishers, New York. 462 pp.

PATALAS, K., AND A. SALKI. 1973. Crustacean plankton and the eutrophication of lakes in the Okanagan Valley, British Columbia. J. Fish. Res. Board Can. **30:** 519-542.

PEARSALL, W. H. 1917. The aquatic and marsh vegetation of Esthwaite Water. J. Ecol. **5:** 180-201.

PETTS, G. E. 1984. Impounded rivers, perspectives for ecological management. John Wiley & Sons, Toronto. 326 pp.

RASMUSSEN, J. B., AND J. KALFF. 1987. Empirical models for zooplankton biomass in lakes. Can. J. Fish. Aquat. Sci. **44:** 990 - 1001.

RASMUSSEN, J. B., L. GODBOUT, AND M. SCHALLENBERG. 1989. The humic content of lake water and its relationship to watershed and lake morphometry.

Limnol. Oceanogr. **34:** 1336 - 1343.

RAVEN, P. H., L. R. BERG, AND G. B. JOHNSON. 1993. Environment. Saunders College Publishing, Toronto. 569 pp.

RAWSON, D. S. 1952. Mean depth and fish production of large lakes. Ecology **33:** 513-521.

RICKLEFS, R. E. 1977. Environmental heterogeneity and plant species diversity: a hypothesis. Am. Nat. **111:** 376-379.

RYDER, R. A. 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. **94:** 214-218.

RYDER, R. A., S. R. KERR, L. H. LOFTUS, AND H. A. REGIER. 1974. The morphoedaphic index, a fish yield estimator - review and evaluation. J. Fish. Res. Board Can. **31:** 663-688.

RYDER, R. A. 1982. The morphoedaphic index - use, abuse and fundamental concepts. Trans. Am. Fish. Soc. **111:** 154-164.

SCHINDLER, D. W., F. A. J. ARMSTRONG, S. K. HOLMGREN, AND G. J. BRUNSKILL. 1971. Eutrophication of Lake 227, experimental lakes area, northwestern Ontario, by addition of phosphate and nitrate. J. Fish. Res. Board Can. **28:** 1763-1782.

SOLORZANO, L. 1969. Determination of ammonia in natural waters by phenolhypochlorite method. Limnol. Oceanogr. **14:** 799-801.

SPAIN, J. D. 1982. Basic microcomputer models in biology. Addison-Wesley Publishing Co., Reading Mass. 354 pp.

SPENCE, D. H. N. 1982. The zonation of plants in freshwater lakes. Adv. Ecol. Res. **12:** 37-125.

STATZNER, B., AND H. HIGLER. 1985. Questions and comments on the river continuum concept. Can. J. Fish. Aquat. Sci. **42:** 1038-1044.

STOCKNER, J. G., AND A. C. COSTELLA. 1976. Marine phytoplankton growth in high

concentrations of pulpmill effluent. J. Fish. Res. Board Can. **33:** 2758-2765.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37:** 130-137.

VINSON, M. R., D. K. VINSON, T. R. ANGRADI. 1992. Aquatic macrophytes and instream flow characteristics of a Rocky Mountain river. Rivers **3:** 260-265.

VITT, D. H., Y. LI, AND R. J. BELLAND. 1995. Patterns of bryophyte diversity in peatlands of continental western Canada. The Bryologist **98:** 218-227.

WARD, J. V., AND J. A. STANFORD. 1983. The intermediate-disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. Pages 347-356 *in* T. D. Fontaine and S. M. Bartell [Eds.]. Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, Michigan.

WARRINGTON, P. D. 1980. Studies on aquatic macrophytes part XXXIII : Aquatic plants of British Columbia. Province of British Columbia, Ministry of Environment, Inventory and Engineering Branch, December, 1980.

WELSH, R. P., P. DENNY. 1979. The translocation of ^{32}P in two submerged aquatic angiosperm species. New Phytol. **82:** 645-656.

WETZEL, R. G. 1983. Limnology (2nd edition). Saunders College Publishing, Toronto. 767 pp.

WHITTAKER, R. H. 1972. Evolution and measurement of species diversity. Taxon **21:** 213-251.

WILLIAMS, J. D. H., J. K. SYERS, AND T. W. WALKER. 1967. Fractionation of soil inorganic phosphate by a modification of Chang and Jackson's procedure. Soil Sci. Am. Proc. **31:** 736-739.

YOUNGS, W. D., AND D. G. HEIMBUCH. 1982. Another consideration of the morphedaphic index. Trans. Am. Fish. Soc. **111:**151-153.

Part III. Plant-plant relations in rivers

4. Niche segregation and conspecific interactions in riverine macrophyte communities[1]

Introduction

Studies on riverine macrophytes have largely focused on the relationship between the growth and abundance of macrophytes in relation to abiotic factors such as current velocity (Chambers *et al.* 1991a; Boeger 1992), flow (Bilby 1977) and nutrients (Peverly 1979). By comparison, few studies have investigated relationships between macrophytes and other biota. Moreover, amongst those that have, the focus has largely been on interactions between macrophytes and aquatic animals such as epiphytic invertebrates (Lodge 1985; Downing 1986; Sheldon 1987), benthic invertebrates (Chambers *et al.* 1990; Chambers *et al.* 1991b), insects (Angerilli and Beirne 1980), fishes (Casterlin and Reynolds 1978; Crowder and Cooper 1982; Nichols and Shaw 1986) and waterfowl (Krull 1970). However, despite increasing knowledge regarding macrophyte-animal relations, very little is known about macrophyte-macrophyte interactions.

Submerged macrophytes in large rivers are usually restricted to near-shore regions (e.g., Haslam 1987) where they may form dense bands which can be seen from the air using aerial surveying techniques (French and Chambers 1993). The distance these macrophyte bands extend into the river channel may be limited by current speed, depth, light and/or other environmental gradients that change along river cross-sections. Since suitable macrophyte habitat may be limited to near-shore regions in large rivers, macrophyte species have to coexist in finite space. This would suggest that interspecific competition for environmental resources (e.g.,

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[1]A version of this chapter will be submitted for publication in *Freshwater Biology*

sites of suitable current velocity, light and nutrient concentration) may significantly effect the growth and success of macrophyte species in rivers. However, Butcher (1933), Westlake (1973) and Gregg and Rose (1982) suggest that rather than competing, macrophytes facilitate the further colonization and growth of other macrophytes by acting as barriers to water flow thereby decreasing current velocity and increasing the settling rate of suspended sediments which accumulate within the stand.

The purpose of this study was to: (1) investigate how environmental resources are partitioned amongst the dominant submerged macrophyte taxa in a large river in northern British Columbia, Canada, and (2) test the hypothesis that the presence of macrophytes can facilitate the growth of other macrophytes with an *in situ* experimental approach.

Methods and Materials

Study site, field sampling methods and laboratory analyses

A description of the Nechako River, British Columbia (the river system used in this study), is given in Chapter 2 ("*Study site*" section) of this thesis and, to conserve space and minimize repetition, is not repeated in this chapter. Similarly, the methods used to collect macrophytes and analyze sediments are identical to those described in the "*Field sampling methods*" and "*Laboratory analyses*" sections, respectively, of Chapter 2 and are not repeated in this chapter.

Resource partitioning

Resource partitioning was evaluated for the dominant taxa: *Elodea canadensis* Rich., *Ranunculus aquatilis* L., *Myriophyllum exalbescens* Fern.,

Callitriche hermaphroditica L., *Ceratophyllum demersum* L., *Potamogeton berchtoldii* Fieb., *Potamogeton gramineus* L., *Potamogeton pectinatus* L., *Potamogeton richardsonii* (Bennett) Rydb., *Chara* and aquatic mosses. Three environmental resources were chosen to evaluate niche overlap: (1) depth, (2) current velocity, and (3) bottom sediment grain size. Each resource was grouped with current velocity classified as very slow (0.0-0.2 $m \cdot s^{-1}$), slow (0.2-0.4 $m \cdot s^{-1}$), moderate (0.4-0.6 $m \cdot s^{-1}$) and fast (0.6-1.6 $m \cdot s^{-1}$); grain size as silts (3.9-62.5 μm), sands (62.5-470 μm; *sensu* Gordon *et al.* 1992) and bare rock; and depth as shallow (0.1-1.5 m), moderate (1.5-3.0 m) and deep (3.0-4.5 m). The niche overlap (% overlap) between each species was then calculated for each resource with the Schoener overlap index as described in Krebs (1989):

$$P_{jk} = [\sum_{i=1}^{s} (minimum\ p_{ij}, p_{ik})] \cdot 100 \quad (1)$$

where P_{jk} is the percentage overlap between species j and k, p_{ij} and p_{ik} are the proportion of resource i of the total resources used by species j and species k, and s is the total number of resource states. Due to sample size differences between each resource state, it was necessary to standardize n prior to calculating biomass proportions (p_{ij} and p_{ik}). To standardize, n was first summed for all resource states to give the total number of samples (N). Then $n_{std.}$ was determined by dividing N by the number of resource states (s). The standardized total biomass within each resource state was then determined by multiplying $n_{std.}$ by the observed biomass within each resource state and dividing through by n.

In situ interaction experiment

An ~ 800 m reach of the Nechako River near the Village of Fort Fraser was selected as the site to test the hypothesis that the presence of macrophytes can

facilitate the growth of other macrophytes. This area was selected as it had monospecific and discrete stands (patches) of *E. canadensis* (biomass 366±11 $g \cdot m^{-2}$; mean±1 S.E.) which extended well out into the river channel (Fig. 1). The sediments within the patches were muddy and several centimetres deep whereas between patches, the river bottom was composed of cobbles with no observable sediment layer, suggesting that the patches of *E. canadensis* caused localized decreases in current speed, resulting in the deposition and accumulation of fine sediments.

Plastic trays (45 × 33 × 11 cm deep, inside measures) were divided widthwise in half with aluminum strapping. Half of each tray was filled (to ~ 8 cm deep) with homogenized sediments collected from within patches of *E. canadensis* (hereafter called the sediment treatment), with the other half being filled with cobbles collected from between the patches (cobble treatment). Ten individual *E. canadensis*, between 10 and 15 cm in length, with healthy roots were planted into each half of each tray. The trays were then placed in a backwater area for 1 week prior to the start of the experiment to allow the plants to establish their rooting systems. In mid August 1992, eight patches were located. One tray was placed near the centre of each patch and another ~ 2 m to the outside of each patch. The trays were dug into the riverbed to ensure that they would not be swept away by currents. The trays remained in place for one year and were retrieved in mid August 1993. Following retrieval, the plants were rinsed with tap water to remove debris, sorted to species with keys in Warrington (1980), dried to constant weight at 80°C and weighed to 0.01 g. Sediments were collected from each side of each tray and frozen until analyzed for exchangeable phosphorus (P) concentrations. Exchangeable P concentrations were determined from frozen sediment samples after they were thawed to room temperature. Duplicate samples from within each side of each tray were pooled prior to analysis; all analyses were performed in

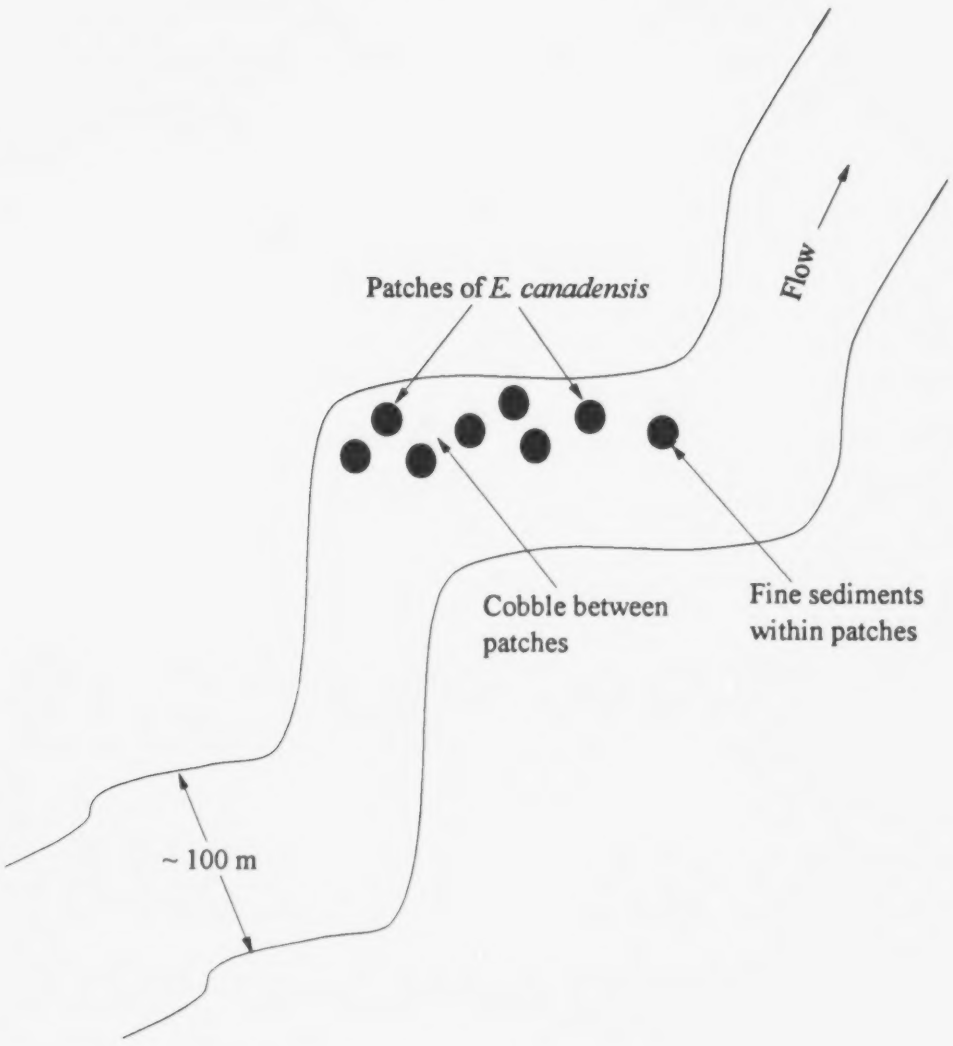

FIGURE 1. Schematic of the site where the *in situ* interaction experiment was undertaken (near Fort Fraser- see Fig. 1, Chapter 2) showing patches of *E. canadensis* and associated substrate types.

duplicate. Exchangeable P was extracted from approximately 0.25 g of homogenized wet sediment by shaking (16 h) in 25 ml of 0.1 N NaOH + 0.1 N NaCl (after Williams *et al.* 1967) and measured spectrophotometrically (Murphy and Riley 1962). Bare cobble was assumed to have no exchange capacity for P.

Results

Resource partitioning

Macrophytes were found to occupy up to 46% of the river's channel, but were usually restricted to near-shore regions such that, on average, 12±3% of the riverbed across the channel was covered with macrophytes. Within the zone of macrophyte colonization, there was considerable physical heterogeneity with respect to sediment properties, depth and current speed with sediment grain size ranging from fine silts (3.9 μm) to bare rock, depth from nil to 4.5 m and current speed from 0.0 to 1.6 $m \cdot s^{-1}$. Macrophyte taxa appeared to inhabit different microenvironments within the river's littoral zone with some taxa being highly specific to certain environmental conditions. For example, *C. demersum* was found almost exclusively (> 98% of it's total biomass, TB) at sites with current speeds < 0.2 $m \cdot s^{-1}$, moderate depths (1.5-2.0 m) and silty substrates (14-56 μm) whereas mosses were most prevalent at sites with current speeds > 0.6 $m \cdot s^{-1}$ (95% TB), depths < 1.5 m (98% TB) and substrates of bare rock (76% TB) (Table 1). *C. hermaphroditica* and *P. gramineus*, while not as specific as mosses and *C. demersum* for particular current speeds and substrates, were almost always found at depths < 1.5 m (Table 1).

Comparisons of niche overlap showed that mosses and *C. demersum* had completely different niches with their niche overlap (NO) being only 3, 3 and 5%

TABLE 1. Corrected proportion (% total mass sampled) of each taxa observed in categories of current speed ($m \cdot s^{-1}$), depth (m) and sediment grain size (μm) in the Nechako River, British Columbia, Canada.

Species	Current speed ($m \cdot s^{-1}$)				Depth (m)			Grain size (μm)		
	0.0-0.2	0.2-0.4	0.4-0.6	>0.6	0.1-1.5	1.5-3.0	3.0-4.5	Silt (14-56)	Sand (63-470)	Bare rock
E. canadensis	62	37	1	0	28	72	0	83	17	0
P. richardsonii	82	17	1	0	18	37	45	84	16	0
M. exalbescens	86	12	3	0	64	35	0	86	14	0
C. demersum	99	1	0	0	2	98	0	99	1	0
P. pectinatus	89	9	2	0	84	15	0	69	31	0
P. berchtoldii	78	22	0	0	76	23	0	49	51	0
Mosses	3	2	0	95	98	1	0	4	19	76
R. aquatilis	15	23	62	0	35	65	0	26	71	4
P. gramineus	54	43	3	0	83	17	0	66	34	0
C. hermaphroditica	63	36	0	2	99	1	0	57	43	0
Chara sp.	36	57	7	0	74	25	1	35	65	0

for depth, current speed and sediment grain size, respectively (Tables 2-4). In contrast, other taxa shared some resource states but were segregated by others. For example, *E. canadensis* and *R. aquatilis*, while having an NO of 93% for depth, occupied sites of different current speed (NO = 39%) and sediment texture (NO = 43%) (Tables 2-4). Thus, TB of *R. aquatilis* was 71% and 62% on sandy (63-470 μm) substrates and at moderate current speeds (0.4-0.6 $m \cdot s^{-1}$), respectively, whereas *E. canadensis* was most prevalent at sites with current speeds < 0.2 $m \cdot s^{-1}$ (62% TB) and on silty sediments (83% TB) (Table 1). Likewise, *P. richardsonii* and *M. exalbescens* were found at similar current speeds (NO = 95%) and on similar substrates (NO = 98%), but occupied different depths (NO = 53%) such that 64% of *M. exalbescens'* TB occurred at depths < 1.5 m as compared to 18% for *P. richardsonii* (Tables 1-4). Depth also segregated *P. pectinatus* from *E. canadensis* (NO = 43%) and *C. demersum* (NO = 17%) such that all three species were most abundant at current speeds < 0.2 $m \cdot s^{-1}$ and on silty substrates; but, whereas *E. canadensis* and *C. demersum* were primarily found at depths between 1.5 and 3.0 m, *P. pectinatus* was typically (84% TB) found at depths < 1.5 m (Tables 1-4). Some species occupied very similar niches with respect to all measured environmental variables. For example, the NO for *P. berchtoldii* and *P. gramineus* was 93, 76 and 83% for depth, current speed and sediment grain size, respectively, with both species being most common at sites with current speeds < 0.4 $m \cdot s^{-1}$, depths < 1.5 m and silty to sandy substrates (Tables 1-4). Likewise, both *P. pectinatus* and *M. exalbescens* predominated at sites with very slow (0.0-0.2 $m \cdot s^{-1}$) current speeds, shallow (0.1-1.5 m) depths and silty (14-56 μm) substrates, with NO's of 97, 79 and 83% for these parameters, respectively (Tables 1-4).

Analysis of the relationship between the biomass of the dominant taxa for each substrate type and total plant biomass showed that for silt substrates, biomass of the dominant taxa, *E. canadensis*, increased as the biomass of the stand (i.e.,

TABLE 2. Matrix showing niche overlap (Shoener overlap index, %), in terms of depth (m), for submerged macrophyte taxa in the Nechako River, British Columbia, Canada.

	E. canadensis	*P. richardsonii*	*M. exalbescens*	*C. demersum*	*P. pectinatus*	*P. berchtoldii*	Mosses	*R. aquatilis*	*P. gramineus*	*C. hermaphroditica*	*Chara* sp.
E. canadensis	100	55	63	74	43	51	29	93	45	29	53
P. richardsonii	-	100	53	39	33	41	19	55	35	19	44
M. exalbescens	-	-	100	37	79	87	65	70	81	65	89
C. demersum	-	-	-	100	17	25	3	67	19	3	27
P. pectinatus	-	-	-	-	100	91	85	50	99	85	89
P. berchtoldii	-	-	-	-	-	100	77	58	93	77	97
Mosses	-	-	-	-	-	-	100	36	84	99	75
R. aquatilis	-	-	-	-	-	-	-	100	52	36	60
P. gramineus	-	-	-	-	-	-	-	-	100	84	91
C. hermaphroditica	-	-	-	-	-	-	-	-	-	100	75
Chara sp.	-	-	-	-	-	-	-	-	-	-	100

TABLE 3. Matrix showing niche overlap (Shoener overlap index, %), in terms of current speed ($m \cdot s^{-1}$), for submerged macrophyte taxa in the Nechako River, British Columbia, Canada.

	E. canadensis	*P. richardsonii*	*M. exalbescens*	*C. demersum*	*P. pectinatus*	*P. berchtoldii*	Mosses	*R. aquatilis*	*P. gramineus*	*C. hermaphroditica*	*Chara* sp.
E. canadensis	100	80	75	63	72	84	5	39	92	98	74
P. richardsonii	-	100	95	83	92	95	5	33	72	80	54
M. exalbescens	-	-	100	87	97	90	5	30	69	75	51
C. demersum	-	-	-	100	90	78	3	16	55	64	37
P. pectinatus	-	-	-	-	100	87	5	26	65	72	47
P. berchtoldii	-	-	-	-	-	100	5	37	76	85	58
Mosses	-	-	-	-	-	-	100	6	6	7	5
R. aquatilis	-	-	-	-	-	-	-	100	38	38	45
P. gramineus	-	-	-	-	-	-	-	-	100	90	82
C. hermaphroditica	-	-	-	-	-	-	-	-	-	100	72
Chara sp.	-	-	-	-	-	-	-	-	-	-	100

TABLE 4. Matrix showing niche overlap (Shoener overlap index, %), in terms of sediment grain size (μm), for submerged macrophyte taxa in the Nechako River, British Columbia, Canada.

	E. canadensis	*P. richardsonii*	*M. exalbescens*	*C. demersum*	*P. pectinatus*	*P. berchtoldii*	Mosses	*R. aquatilis*	*P. gramineus*	*C. hermaphroditica*	*Chara* sp.
E. canadensis	100	99	97	84	86	66	21	43	83	74	52
P. richardsonii	-	100	98	85	85	65	20	42	82	73	51
M. exalbescens	-	-	100	87	83	63	18	40	80	71	49
C. demersum	-	-	-	100	70	50	5	27	67	58	45
P. pectinatus	-	-	-	-	100	80	23	57	97	88	66
P. berchtoldii	-	-	-	-	-	100	23	77	83	92	86
Mosses	-	-	-	-	-	-	100	27	23	23	23
R. aquatilis	-	-	-	-	-	-	-	100	60	69	91
P. gramineus	-	-	-	-	-	-	-	-	100	91	69
C. hermaphroditica	-	-	-	-	-	-	-	-	-	100	78
Chara sp.	-	-	-	-	-	-	-	-	-	-	100

total community) increased ($r = 0.95$; $P < 0.0001$) (Fig. 2). In contrast the species dominating sites with sandy substrates (i.e., *R. aquatilis*) and bare rock substrates (e.g., mosses) were most abundant where the biomass of the stand was low (Fig. 2).

In situ interaction experiment

E. canadensis attained biomasses of 17.7±5.1 g and 14.6±3.8 g for the cobble and sediment treatments, respectively, when grown within a macrophyte patch. In contrast, *E. canadensis* biomass was only 0.3±0.3 g and 0.0±0.0 g for the cobble and sediment treatments, respectively, when grown outside a macrophyte stand (Fig. 3). Analysis of variance showed no significant ($P = 0.61$) affect of sediment type on biomass, but a significant ($P < 0.0001$) effect of position (within verses outside the patch). The lack of an affect due to sediment type was due to the sediment conditions at the end of the experiment. While all trays had sediment and cobble sections at the start, sediments accumulated in the trays positioned within the macrophytes patches and were scoured from the trays positioned outside the patches. Thus, at the end of the experiment, exchangeable P concentrations from trays located within macrophyte stands were 452±74 and 370±31 $\mu g \cdot g^{-1}$ for sediment and cobble treatments, respectively (Fig. 4). There was little, if any, sediment present in either the sediment or cobble treatments positioned outside patches.

Discussion

In the Nechako River, British Columbia, 11 common taxa and 3 rare taxa of aquatic macrophytes co-occur in the near-shore zone (i.e., a distance equivalent on average to 12% of the river's width). However, physical variability within this

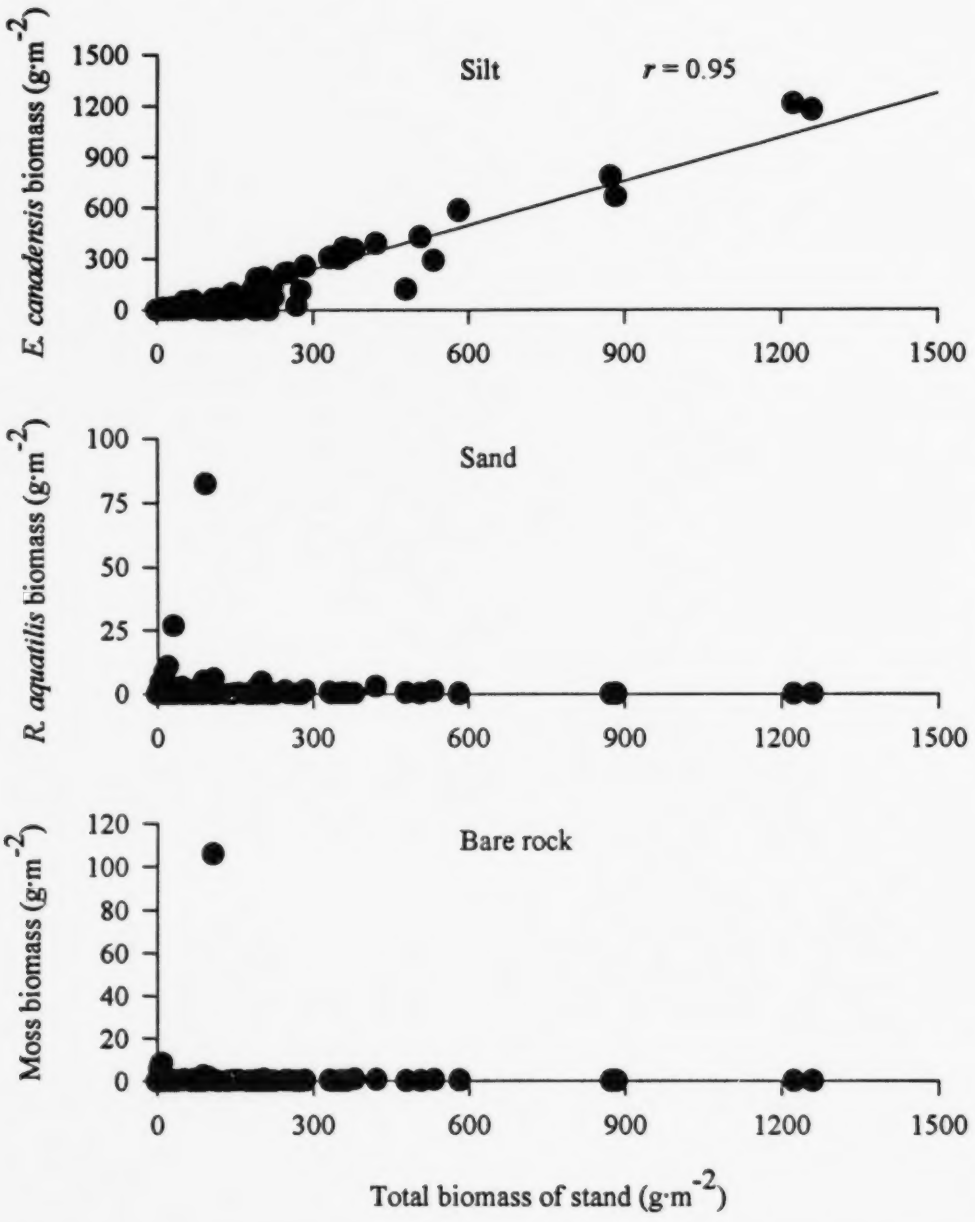

FIGURE 2. Relationships between biomass ($g \cdot m^{-2}$) of the total stand and the dominate taxa for sites with silty substrates (*E. canadensis*), sandy substrates (*R. aquatilis*) and bare rock substrates (mosses).

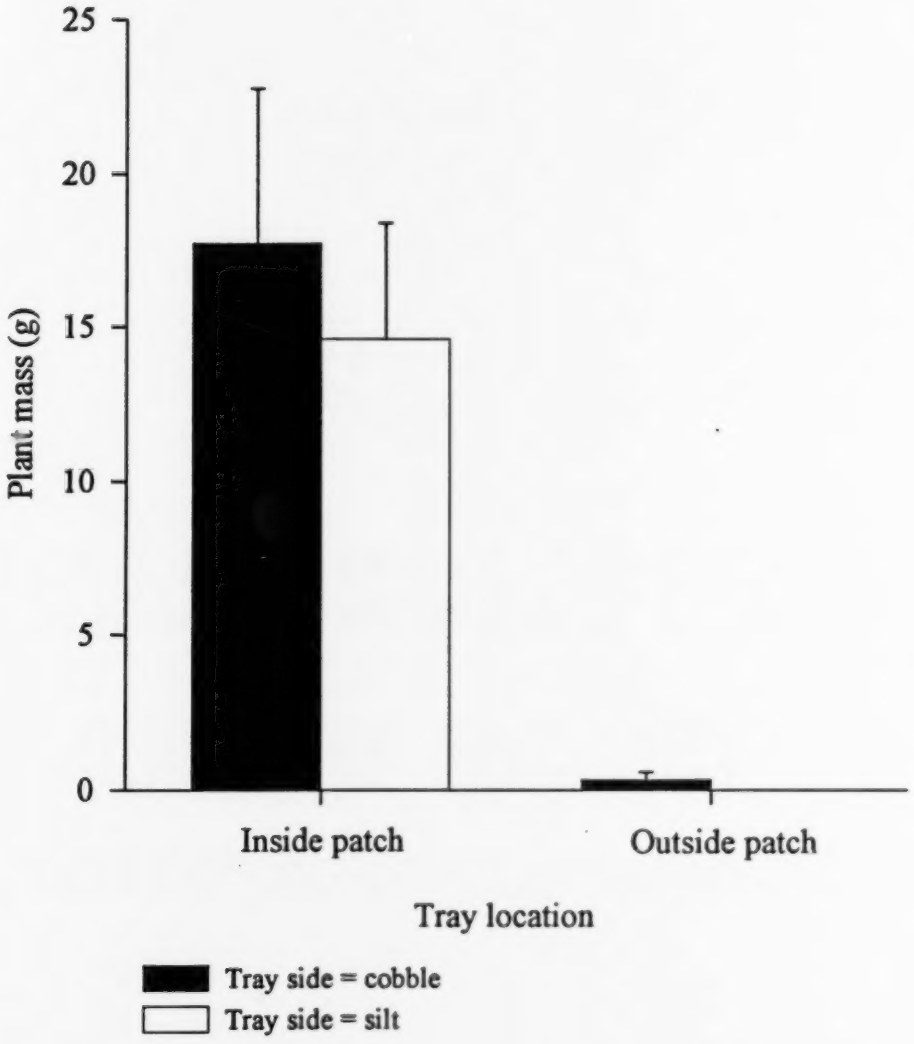

FIGURE 3. *E. canadensis* biomass (g) from trays containing cobble and silt substrates placed both inside and outside of *E. canadensis* patches.

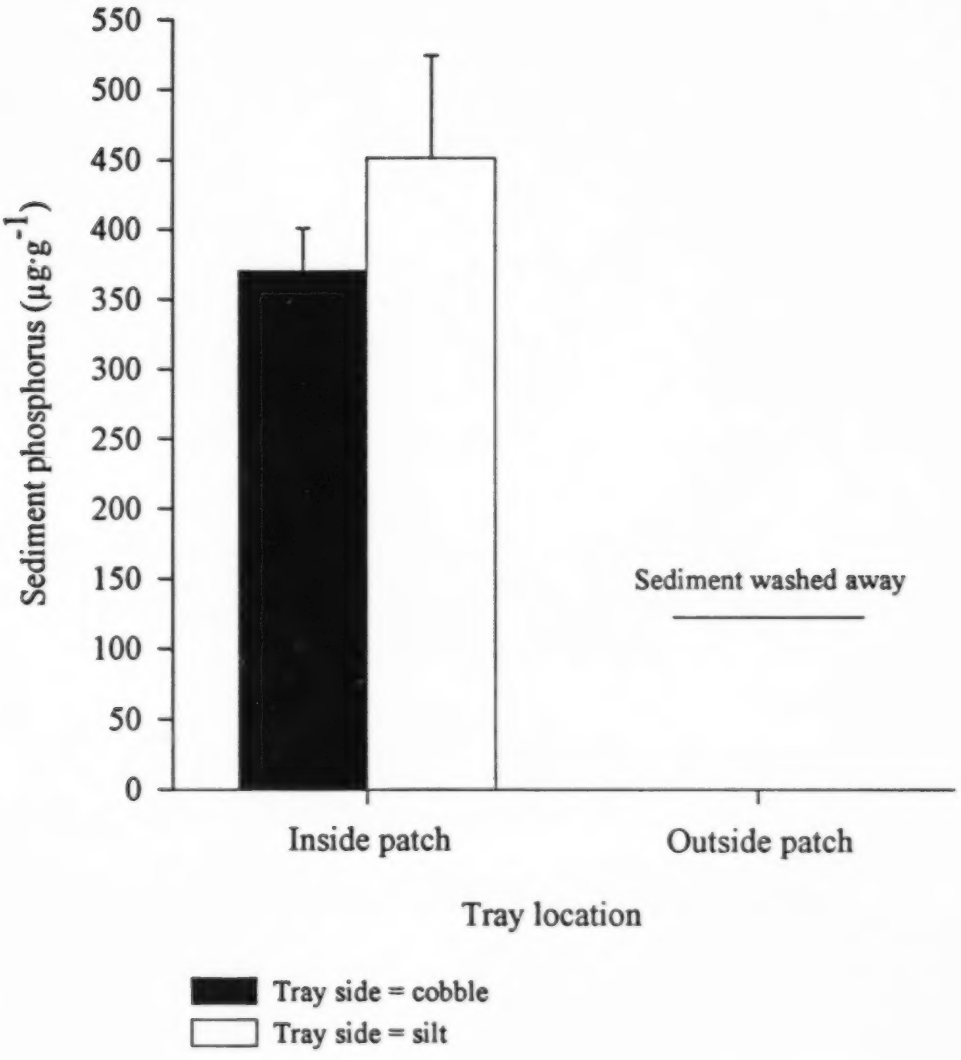

FIGURE 4. Sediment exchangeable phosphorus concentrations ($\mu g \cdot g^{-1}$) at the end of the experiment for treatments inside and outside of *E. canadensis* patches.

zone created a variety of niches, thus allowing several taxa to coexist with often very few resource states in common (Tables 1-4). Analyses of species abundance in relation to physical gradients within the near-shore zone showed that gradients of current speed, substrate texture and depth determined the relative distribution and abundance of macrophytic taxa. The segregation of macrophyte taxa along environmental gradients has also been observed by other researchers. Glime and Vitt (1987) reported that fast-flowing montane streams often have few vascular macrophytes but can have extensive moss communities. Likewise, Bilby (1977) found that *E. canadensis* was restricted to slow current speeds in Fall Creek, New York, whereas *Potamogeton crispus* was common in faster waters. Haslam (1987) reported that in rivers of Europe, *Ranunculus* spp. are common in regions of high current speed and prefer sandy sediments over silts and clays. However, while other researchers have reported the taxonomic segregation of riverine macrophyte species along gradients of current speed and sediment texture, this study showed that some taxa may also be specific to particular depths. For example, *C. hermaphroditica* (99% TB), mosses (98% TB), *P. pectinatus* (84% TB) and *P. gramineus* (83% TB) were largely confined to depths < 1.5 m (Table 1). *C. hermaphroditica* was also specific to a particular depth strata, being most abundant (98% TB) at depths between 1.5 and 3.0 m (Table 1). While few, if any, studies have reported depth-related segregation amongst macrophyte species in lotic systems, evidence from lake-studies suggests that depth partitioning may occur. For example, Chambers and Kalff (1987) using an *in situ* experimental approach in Lake Memphremagog, Quebec/Vermont, found differences in the way *Potamogeton praelongus*, *Vallisneria americana*, and *Potamogeton robbinsii* responded to depth. Similarly, Sheldon and Boylen (1977), in a study of 28 macrophyte species in Lake George, New York, observed that *P. pectinatus* was most abundant at shallow depths (1 m) where *E. canadensis* was abundant at depths to 7 m.

Differences in the way macrophyte taxa are distributed along physical gradients have been attributed to morphological and physiological adaptations. Thus, *E. canadensis*, having delicate leaves, a fragile stem (Dale 1957) and a relatively weak rooting system (Bilby 1977; Madsen and Adams 1989) is considered to be poorly adapted to fast-flowing environments. By comparison, the vertically compressed, cushion-like growth form of aquatic mosses (Butcher 1933) may allow them to colonize sites with abrasive currents, while their dependence on water-column nutrients (Glime and Vitt 1984) can permit growth on bare rock. Using the morphological adaptation premise, it is possible that the spindly growth form (i.e., thin stem and finely dissected leaves) of *R. aquatilis* is an adaptation to fast currents as it may minimize the friction between plant and water, thereby reducing mechanical damage to plant tissues. However, morphology alone cannot account for the distribution of all taxa in the Nechako River. For example, while tall species with "bushy", unstreamlined growth forms (e.g., *E. canadensis*, *P. richardsonii*, *M. exalbescens* and *C. demersum*) were most abundant at sites with current speeds < 0.2 $m \cdot s^{-1}$ and cushion-like (e.g., mosses) and spindly (e.g., *R. aquatilis*) growth forms predominated at sites with current speeds > 0.4 $m \cdot s^{-1}$, some streamline species (e.g., *P. pectinatus* and *P. berchtoldii*) were found at sites with very slow currents (< 0.2 $m \cdot s^{-1}$; Table 1). This suggests that while bushy growth forms may confine some species to slow waters, species with a streamlined growth form are not necessarily specific to fast waters.

While macrophyte species can partition their physical environment so as to avoid or reduce niche overlap, results of the *in situ* experiment demonstrated that the presence of *E. canadensis* can facilitate the growth of conspecifics. Thus, the introduction of young *E. canadensis* shoots into a mature stand resulted in significant growth compared to very little growth for similar shoots placed outside the stand (Fig. 3). The finding, after 1 year, that *E. canadensis* biomass and

exchangeable P concentrations were similar for both treatment compartments of inside-patch trays indicates that *E. canadensis* facilitates the growth of conspecifics by increasing the deposition rate of fine nutrient-rich sediments. In contrast, sediments were scoured from sediment treatments and siltation did not occur in cobble treatments of outside-patch trays (Fig. 4). These findings are consistent with those of Madsen and Warncke (1983) who showed that the submersed angiosperm *Callitriche stagnalis* can decrease current speed by up to 92%. Thus, the decrease in current speed associated with the presence of macrophytes can result in fine-sediment deposition (Butcher 1933; Gregg and Rose 1982). However, in contrast to our observation that macrophytes can facilitate the growth of conspecifics, Moen and Cohen (1989) reported that the growth rate of *P. pectinatus* and *M. exalbescens* decreased with increasing density of conspecifics. This discrepancy may relate to the fact that Moen and Cohen (1989) undertook their experiments in small, closed-system aquaria where essential resources (i.e., nutrients) were not replenished whereas our experiment was performed *in situ* in an open, flowing system where nutrients were continually added to the experimental units through deposition, thus minimizing intraspecific competition for nutrients and substrate. The observation that the biomass of *E. canadensis*, a species which was most prevalent at sites with silty substrates (83% TB) and slow current speeds (99% TB; Table 1), was greater within high-biomass stands than within low-biomass stands ($r = 0.98$; $P < 0.0001$) further supports the hypothesis that macrophytes can facilitate the growth of other macrophytes (Fig. 2). However, this pattern was not evident for taxa which dominated faster waters with sandy or bare rock substrates. Thus, biomasses of *R. aquatilis* and mosses were greater in low-biomass stands (Fig. 2). A similar observation was reported by Westlake (1973) where *Ranunculus calcareus* died back in a shallow chalk stream following increases in stand density. Westlake (1973) attributed the recession of *R.*

calcareous to the decrease in current speed resulting from increased stand density which, in turn, promoted the accumulation of fine sediments and the colonization of the emergent macrophyte *Rorippa nasturtium-aquaticum* which is adapted to slow-moving waters with fine substrates. *R. nasturtium-aquaticum* eventually excluded *R. calcareus* by blocking solar irradiance. This suggests that only macrophytes adapted to efficiently exploit silt substrates (e.g., *E. canadensis*) facilitate the colonization and growth of conspecifics in flowing waters. Species adapted to exploit coarse substrates (e.g., *R. aquatilis*) would likely dominate early successional stages of macrophyte communities in rivers and, by creating suitable habitat through slowing current speed and increasing the deposition rate of fine sediments, would allow the encroachment of species which can compete more effectively in high-nutrient environments. While this species turnover (i.e., from a community dominated by *R. aquatilis* to one dominated by *E. canadensis*) can occur over one growing season (e.g., Westlake 1973), in regulated rivers with severely reduced flows, such as the Nechako River, silty bottom sediments may not be scoured annually as they are in most natural rivers (Ham *et al.* 1981) and thus species such as *E. canadensis* may dominate over several seasons, or until sufficient disturbance scours them away. Thus, *E. canadensis* has dominated the upper reaches of the Nechako River, where freshet flows are minimal, over the entire 1991 to 1993 growing seasons.

In conclusion, this study showed that macrophyte species in large rivers can be segregated by current speed, substrate texture and depth and that species able to compete well in nutrient rich environments may facilitate the colonization and growth of conspecifics. The finding that macrophyte species are segregated by physical and chemical gradients (Tables 1-4) in rivers is consistent with current evolutionary theory which holds that selection pressure drives species within a community to partition essential resources so as to minimize competition (Barbour

et al. 1987). Alternatively, the observed species distribution could be due to establishment processes. Angiosperm species may vary in their ability to colonize particular habitats via sexual reproduction. Thus, species with low-mass seeds are most likely to colonize regions of low current velocity than regions of high current velocity since high velocities may keep low-mass seeds in suspension. Conversely, species with high-mass seeds may colonize regions of greater current velocity. In this view, the observed species distribution may be the result of establishment processes and may not reflect competitive interactions. However, given that aquatic angiosperms proliferate predominately through rhizomatous growth in lotic systems it is more likely that the observed distribution evolved via species interactions and habitat selectivity.

References Cited

ANGERILLI, N. P. D., AND B. P. BEIRNE. 1980. Influences of aquatic plants on colonization of artificial ponds by mosquitoes and their insect predators. Can. Entomol. **112:** 793-796.

BARBOUR, M. G., J. H. BURKE, AND W. D. PITTS. 1987. Terrestrial plant ecology (2nd Edition). The Benjamin/Cummings Publishing Company, Inc., Don Mills, Ontario. 634 pp.

BILBY, R. 1977. Effects of spate on the macrophyte vegetation of a stream pool. Hydrobiologia **56:** 109-112.

BOEGER, R. T. 1992. The influence of substratum and water velocity on the growth of *Ranunculus aquatilis* L. (Ranunculaceae). Aquat. Bot. **42:** 351-359.

BUTCHER, R. W. 1933. Studies on the ecology of rivers. I. On the distribution of

macrophytic vegetation in the rivers of Britain. J. Ecol. **21:** 58-91.

CASTERLIN, M. E., W. W. REYNOLDS. 1978. Habitat selection by juvenile bluegill sunfish, *Lepomis macrochirus*. Hydrobiologia **59:** 75-79.

CHAMBERS, P. A., J. M. HANSON, J. M. BURKE, AND E. E. PREPAS. 1990. The impact of the crayfish *Orconectes virilis* on aquatic macrophytes. Freshwater Biol. **24:** 81-91.

CHAMBERS, P. A., J. M. HANSON, AND E. E. PREPAS. 1991b. The effect of aquatic plant chemistry and morphology on feeding selectivity by the crayfish, *Orconectes virilis*. Freshwater Biol. **25:** 339-348.

CHAMBERS, P. A., AND J. KALFF. 1987. Light and nutrients in the control of aquatic plant community structure. I. *In situ* experiments. J. Ecol. **75:** 611-619.

CHAMBERS, P. A., E. E. PREPAS, H. R. HAMILTON, AND M. L. BOTHWELL. 1991a. Current velocity and its effect on aquatic macrophytes in flowing water. Ecol. Appl. **1:** 249-257.

CROWDER, L. B., AND W. E. COOPER. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology **63:** 1802-1813.

DALE, H. M. 1957. Developmental studies of *Elodea canadensis* Michx. II. Experimental studies on morphological effects of darkness. Can. J. Bot. **35:** 51-64.

DOWNING, J. A. 1986. A regression technique for estimation of epiphytic invertebrate populations. Freshwater Biol. **16:** 161-173.

ENVIRONMENT CANADA. 1991. Historical streamflow summary, British Columbia, to 1990. Environment Canada, Inland Waters Directorate, Water Resources Branch, Water Survey of Canada, Ottawa, Canada.

FRENCH, T. D., AND P. A. CHAMBERS. 1993. Aquatic macrophytes in the

Nechako River, British Columbia: Part II. Environmental factors regulating the growth of aquatic macrophytes. National Hydrology Research Institute, Environment Canada, Saskatoon, Saskatchewan, NHRI Contribution No. CS-93993.

GLIME, J. M., AND D. H. VITT. 1984. The physiological adaptations of aquatic Musci. Lindbergia **10:** 41-52.

GLIME, J. M., AND D. H. VITT. 1987. A comparison of bryophyte species diversity and niche structure of montane streams and streambanks. Can. J. Bot. **65:** 1824-1837.

GORDON, N. D., T. A. MCMAHON, AND B. L. FINLAYSON. 1992. Stream hydrology, an introduction for ecologists. John Wiley & Sons, Toronto. 526 pp.

GRAY, D. M. 1973. Handbook on the principles of hydrology: A general text with special emphasis on Canadian conditions. Secretariate, Canadian National Committee for the International Hydrological Decade.

GREGG, W. W., AND F. L. ROSE. 1982. The effects of aquatic macrophytes on the stream microenvironment. Aquat. Bot. **14:** 309-324.

HAM, S. F., J. F. WRIGHT, AND A. D. BERRY. 1981. Growth and recession of aquatic macrophytes on an unshaded section of the River Lambourn, England, from 1971 to 1976. Freshwater Biol. **11:** 381-390.

HASLAM, S. M. 1987. River plants of western Europe. Cambridge University Press, Cambridge, U. K. 396 pp.

KREBS, C. J. 1989. Ecological methodology. Harper and Collings Publishers, New York, NY. 654 pp.

KRULL, J. N. 1970. Aquatic plant-macroinvertebrate associations and waterfowl. J. Wildl. Manage. **34:** 707-718.

LODGE, D. M. 1985. Macrophyte-gastropod associations: observations and

experiments on macrophyte choice by gastropods. Freshwater Biol. **15:** 695-708.

MADSEN, J. D., AND M. S. ADAMS. 1989. The distribution of submerged aquatic macrophyte biomass in a eutrophic stream, Badfish Creek: the effect of environment. Hydrobiologia **171:** 111-119.

MADSEN, T. V., AND E. WARNCKE. 1983. Velocities of currents around and within submerged aquatic vegetation. Arch. Hydrobiol. **97:** 389-394.

MOEN, R. A., AND Y. COHEN. 1989. Growth and competition between *Potamogeton pectinatus* L. and *Myriophyllum exalbescens* Fern. in experimental ecosystems. Aquat. Bot. **33:** 257-270

MURPHY, J. A., AND J. L. RILEY. 1962. A modified single solution method for the determination of inorganic phosphate in natural waters. Anal. Chim. Acta. **27:** 31-36.

NICHOLS, S. A., AND B. H. SHAW. 1986. Ecological life histories of the three aquatic nuisance plants, *Myriophyllum spicatum*, *Potamogeton crispus* and *Elodea canadensis*. Hydrobiologia **131:** 3-21.

PEVERLY, J. H. 1979. Elemental distribution and macrophyte growth downstream from an organic soil. Aquat. Bot. **7:** 319-338.

SHELDON, S. P. 1987. The effects of herbivorous snails on submerged macrophyte communities in Minnesota Lakes. Ecology **68:** 1920-1931.

SHELDON, R. B., AND C. W. BOYLEN. 1977. Maximum depth inhabited by aquatic vascular plants. Am. Midl. Nat. **97:** 248-254.

WARRINGTON, P. D. 1980. Studies on aquatic macrophytes part XXXIII: Aquatic plants of British Columbia. Province of British Columbia, Ministry Environment, Inventory and Engineering Branch, December, 1980.

WESTLAKE, D. F. 1973. Aquatic macrophytes in rivers: a review. Pol. Arch. Hydrobiol. **20:** 31-40.

WILLIAMS, J. D. H., J. K. SEYERS, AND T. W. WALKER. 1967. Fractionation of soil inorganic phosphate by a modification of Chang and Jackson's procedure. Soil Sci. Am. Proc. **31:** 736-739.

Part IV. Summary

5. Major Conclusions

The objective of this project was to quantify the environmental factors regulating the biomass, distribution and species composition of lotic macrophyte communities and to use this basic information as a basis to predict changes in macrophyte community structure resulting from reduced-flow conditions. It was found that the distribution of macrophytes in rivers is controlled by current speed, sediment texture, sediment nitrogen and phosphorus concentrations, and depth (Chapter 2). Both small scale (near shore cross-sectional slope) and large scale (catchment area and longitudinal slope) morphometry were also shown to be important determinants of macrophyte community structure in lotic environments (Chapter 3). Analyses of macrophyte species abundance in relation to physical characteristics of the littoral zone showed that gradients of current speed, sediment texture and depth determined the relative abundance of macrophyte taxa such that macrophyte species inhabited different microenvironments within the river's littoral zone (Chapter 4). The findings of this research have several implications when considering the ecological impacts of river impoundment activities on riverine macrophyte communities, which include the following.

(1) Flow reductions can result in significant increases in macrophyte abundance

In Chapter 2 it was shown that bottom cover (r^2 = 0.80) and cross-sectional biomass (r^2 = 0.82) are inversely correlated with mean summer channel speed. Thus, reductions in channel speed resulting from decreased flow can result in increased macrophyte abundance. This prediction is supported by observations made in the Sutlej River, India, the Volta River, Ghana, the Zambezi River, Rhodesia, the Tuolumne River, California (Petts 1984) and the Otra River, Norway (Rorslett 1988) where substantial increases in macrophyte abundance have been

observed since their impoundment.

(2) Decreases in discharge variability can result in decreased species diversity

In Chapter 3 it was shown that the diversity of macrophyte communities is positively correlated with temporal discharge variability (which is a function of catchment area). This finding is supported by the river continuum concept (Vannote *et al.* 1980) and the intermediate disturbance hypothesis (Connell 1978; Ward and Stanford 1983) which indicate that species diversity increases with increasing environmental heterogeneity or variability. Thus, decreases in temporal discharge variability caused by river diversion projects may result in losses in macrophyte species diversity.

(3) Decreases in discharge may have species-specific impacts

The research presented in Chapter 4 showed that macrophyte taxa are segregated by current speed, sediment texture and depth. Thus, changes in current speed, bottom sediment texture and depth caused by river impoundment may be expected to have species-specific impacts.

References Cited

PETTS, G. E. 1984. Impounded rivers, perspectives for ecological management. John Wiley and Sons, Toronto. 326 pp.

RORSLETT, B. 1988. Aquatic weed problems in a hydroelectric river: the R. Otra, Norway. Regul. Rivers Res. & Manage. **2:** 25-37.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37:** 130-137.

WARD, J. V., AND J. A. STANFORD. 1983. The intermediate-disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. Pages 347-356 *in* T. D. FONTAINE AND S. M. BARTELL [Eds.]. Dynamics of lotic systems. Ann Arbor Science Publishers, Ann Arbor, Michigan.

Part V. Appendices

APPENDIX A: Macrophyte survey data collected in August 1992 for sites in the Nechako River, British Columbia.

Legend:

1. Mercator coordinates = Universal transverse mercator grid coordinate as read from 1:50000 map (location of site)
2. Dist. = distance from shore sample collected from (m)
3. Shore = left (0) or right (1) bank of river when looking upstream
4. Quadrat = n of 3 replicates taken at each sampling interval
5. E. can. = *Elodea canadensis*
6. P. rich. = *Potamogeton richardsonii*
7. M. exalb. = *Myriophyllum exalbescens*
8. C. dem. = *Ceratophyllum demersum*
9. R. aquat. = *Ranunculus aquatilis*
10. P. pect. = *Potamogeton pectinatus*
11. P. gram. = *Potamogeton gramineus*
12. S. cun. = *Sagittaria cuneatus*
13. C. herm. = *Callitriche hermaphroditica*
14. P. berch. = *Potamogeton berchtoldii*
15. L. aquat. = *Limosella aquatica*
16. Chara = *Chara*
17. Mosses = moss
18. Misc. = miscellaneous macrophytes or parts of macrophytes that could not be identified

Appendix A

MERCATOR COORDINATES	Dist. (M)	SHORE	QUADRAT (X OF 3)	E.can. (g/m2)	P. rich. (g/m2)	M. exalb. (g/m2)	C. dem. (g/m2)	R. aquat (g/m2)	P. pect. (g/m2)	P. gram. (g/m2)	S. can. (g/m2)	C. herm. (g/m2)	P. berch. (g/m2)	L. aquat. (g/m2)	Chara (g/m2)	Mosses (g/m2)	Misc. (g/m2)
27760	5	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27760	5	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27760	5	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27760	10	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27760	10	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27760	10	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27760	5	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	16.32	0.00
27760	5	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27760	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.00	0.00
27760	10	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27760	10	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27760	10	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27772	5	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.76	0.00
27772	5	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00
27772	5	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.65	0.00
27772	10	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27772	10	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27772	10	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27772	5	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27772	5	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27772	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27772	10	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27772	10	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27772	10	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29745	5	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29745	5	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29745	5	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29745	5	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29745	5	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29745	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36728	5	0	1	0.00	18.69	0.00	0.00	0.00	207.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix A

MERCATOR COORDINATES	Dist. (M)	SHORE	QUADRAT (X OF 3)	E.can. (g/m2)	P. rich. (g/m2)	M. exalb. (g/m2)	C. dem. (g/m2)	R. aquat (g/m2)	P. pect. (g/m2)	P. gram. (g/m2)	S. cun. (g/m2)	C. herm. (g/m2)	P. berch. (g/m2)	L. aquat. (g/m2)	Chara (g/m2)	Mosses (g/m2)	Misc. (g/m2)
36728	5	0	2	0.00	37.58	0.00	0.00	0.00	50.04	0.00	0.00	0.10	0.59	0.00	0.00	0.00	1.19
36728	5	0	3	0.00	0.20	0.00	0.00	0.00	122.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36728	10	0	1	0.00	0.00	0.00	0.00	0.00	79.81	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36728	10	0	2	26.51	0.00	0.00	0.00	0.00	49.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36728	10	0	3	0.00	0.00	0.00	0.00	0.00	122.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36728	15	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36728	15	0	2	0.00	0.00	0.00	0.00	0.00	9.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36728	15	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36728	20	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36728	20	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36728	20	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36728	5	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36728	5	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36728	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
39752	5	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
39752	5	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
39752	5	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
39752	5	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
39752	5	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
39752	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
124773	5	0	1	0.00	11.37	0.00	0.00	0.00	4.95	44.21	0.00	0.00	52.12	0.00	0.00	0.00	20.47
124773	5	0	2	0.00	20.57	27.40	0.00	0.00	33.13	0.99	0.00	0.00	165.95	0.00	0.40	0.00	11.77
124773	5	0	3	0.20	30.16	168.62	0.00	0.00	22.15	5.84	0.00	0.00	25.62	0.00	0.00	0.20	8.70
124773	10	0	1	18.20	50.44	1.98	0.00	0.00	5.44	0.00	0.00	0.00	13.94	0.00	0.00	0.00	27.69
124773	10	0	2	14.04	27.30	0.00	0.00	0.00	39.96	0.00	0.00	0.00	6.23	0.00	0.00	0.00	11.57
124773	10	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	34.81	0.00	0.00	0.00	0.00
124773	15	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
124773	15	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
124773	15	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
124773	5	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
124773	5	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix A

MERCATOR COORDINATES	Dist. (M)	SHORE	QUADRAT (X OF 3)	E.can. (g/m2)	P. rich. (g/m2)	M. exalb (g/m2)	C. dem. (g/m2)	R. aquat (g/m2)	P. pect. (g/m2)	P. gram. (g/m2)	S. cun. (g/m2)	C. herm. (g/m2)	P. berch. (g/m2)	L. aquat. (g/m2)	Chara (g/m2)	Mosses (g/m2)	Misc. (g/m2)
124773	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
124773	10	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
124773	10	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
124773	10	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
124773	15	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
124773	15	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
124773	15	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
144773	5	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
144773	5	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.00	0.00	0.00	0.00
144773	5	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20
144773	10	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
144773	10	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
144773	10	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
144773	5	1	1	0.10	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.40	0.30	0.00	0.00	0.00
144773	5	1	2	0.00	0.00	0.00	0.00	1.29	0.00	1.58	0.00	0.00	0.20	0.49	0.00	21.26	0.00
144773	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.14	0.00
144773	10	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
144773	10	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
144773	10	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
153911	5	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
153911	5	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
153911	5	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
153911	5	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
153911	5	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
153911	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
157912	5	0	1	462.16	6.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00
157912	5	0	2	251.70	38.97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
157912	5	0	3	288.19	40.35	0.00	0.00	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
157912	10	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
157912	10	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
157912	10	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix A

MERCATOR COORDINATES	Dist. (M)	SHORE	QUADRAT (X OF 3)	E.can. (g/m2)	P. rich. (g/m2)	M. exalb. (g/m2)	C. dem. (g/m2)	R. aquat (g/m2)	P. pect. (g/m2)	P. gram. (g/m2)	S. cun. (g/m2)	C. herm. (g/m2)	P. berch. (g/m2)	L. aquat. (g/m2)	Chara (g/m2)	Mosses (g/m2)	Misc. (g/m2)
157912	5	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
157912	5	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
157912	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
161912	5	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
161912	5	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
161912	5	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
161912	5	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
161912	5	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
161912	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
165910	5	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
165910	5	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
165910	5	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
165910	5	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
165910	5	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
165910	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
269891	5	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
269891	5	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
269891	5	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
269891	5	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
269891	5	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
269891	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
315859	5	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
315859	5	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
315859	5	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
315859	10	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
315859	10	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
315859	10	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
315859	5	1	1	4.25	0.00	0.00	0.00	4.75	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.49	0.00
315859	5	1	2	0.00	0.00	0.00	0.00	5.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
315859	5	1	3	1.19	0.00	0.00	0.00	5.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10
315859	10	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix A

MERCATOR COORDINATES	Dist. (M)	SHORE	QUADRAT (X OF 3)	E.can. (g/m2)	P. rich. (g/m2)	M. exalb. (g/m2)	C. dem. (g/m2)	R. aquat (g/m2)	P. pect. (g/m2)	P. gram. (g/m2)	S. cun. (g/m2)	C. herm. (g/m2)	P. berch. (g/m2)	L. aquat. (g/m2)	Chara (g/m2)	Mosses (g/m2)	Misc. (g/m2)
315859	10	1	2	0.00	0.00	0.00	0.00	2.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
315859	10	1	3	0.00	0.00	0.00	0.00	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
315859	15	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
315859	15	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
315859	15	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
337867	5	0	1	141.72	9.00	0.59	0.00	0.00	0.00	2.57	0.00	0.00	0.20	0.00	0.10	1.68	34.52
337867	5	0	2	221.93	2.27	1.19	0.00	0.69	0.00	0.00	0.00	0.00	0.30	0.00	0.10	0.10	0.00
337867	5	0	3	247.84	32.04	0.20	0.00	0.49	0.00	0.00	0.00	0.00	0.10	0.00	0.10	0.30	29.97
337867	10	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
337867	10	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
337867	10	0	3	45.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
337867	5	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
337867	5	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
337867	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
344863	10	0	1	27.00	11.27	0.00	0.00	0.49	0.00	16.12	0.00	0.00	20.08	0.00	0.00	0.69	0.00
344863	10	0	2	18.49	0.00	0.00	0.00	2.77	0.00	25.42	0.00	0.00	0.00	0.00	0.20	0.20	9.49
344863	10	0	3	0.00	0.00	0.00	0.00	6.03	0.00	25.42	0.00	0.00	0.00	0.00	0.00	0.00	2.57
344863	20	0	1	36.89	0.00	0.00	0.00	3.46	0.00	1.68	0.00	0.00	0.00	0.00	0.00	0.40	0.20
344863	20	0	2	61.71	0.00	0.00	0.00	0.30	0.00	17.80	0.00	0.00	0.00	0.00	0.10	0.69	3.46
344863	20	0	3	81.79	0.00	0.00	0.00	0.20	0.00	23.14	0.00	0.00	0.00	0.00	0.10	1.09	5.04
344863	30	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
344863	30	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
344863	30	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
344863	40	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
344863	40	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
344863	40	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
344863	10	1	1	17.60	0.00	0.00	0.00	17.01	0.00	0.00	0.00	0.00	0.40	0.00	5.04	0.10	2.27
344863	10	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.59
344863	10	1	3	3.96	0.00	0.00	0.00	17.90	0.00	0.00	0.00	0.00	0.30	0.00	1.19	0.10	0.00
344863	20	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
344863	20	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix A

MERCATOR COORDINATES	Dist. (M)	SHORE	QUADRAT (X OF 3)	E.can. (g/m2)	P. rich. (g/m2)	M. exalb. (g/m2)	C. dens. (g/m2)	R. aquat (g/m2)	P. pect. (g/m2)	P. gram. (g/m2)	S. cun. (g/m2)	C. herm. (g/m2)	P. berch. (g/m2)	L. aquat. (g/m2)	Chara (g/m2)	Mosses (g/m2)	Misc. (g/m2)
344863	20	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
356865	10	0	1	0.00	0.00	20.67	6.43	0.69	0.00	0.00	0.00	0.10	0.00	0.00	0.59	0.40	1.09
356865	10	0	2	459.39	2.08	19.88	8.90	2.97	0.00	0.79	0.00	0.10	0.59	0.00	0.79	0.49	16.32
356865	10	0	3	358.51	5.64	29.47	2.67	0.79	0.00	0.00	0.00	0.00	0.10	0.00	0.30	0.10	11.47
356865	20	0	1	11.97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.58	0.00	2.57	0.10	7.02
356865	20	0	2	10.88	0.00	3.56	0.00	6.82	0.00	0.00	0.00	0.00	0.49	0.00	1.19	0.00	3.86
356865	20	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
356865	30	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
356865	30	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
356865	30	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
356865	10	1	1	47.47	83.08	51.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.21
356865	10	1	2	179.60	1.88	1.68	0.00	0.00	0.00	11.47	0.00	0.00	15.03	0.00	0.49	0.00	9.89
356865	10	1	3	19.78	55.68	218.37	0.00	0.00	0.00	40.15	0.00	0.10	2.37	0.00	0.00	0.00	14.84
356865	20	1	1	0.00	454.74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
356865	20	1	2	0.69	182.87	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.10	0.00	0.00
356865	20	1	3	0.79	55.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
356865	30	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
356865	30	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
356865	30	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
356865	40	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
356865	40	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
356865	40	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
357850	5	0	1	1.38	93.26	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.30	0.00	0.00	0.00	0.00
357850	5	0	2	11.67	237.46	9.69	0.00	0.99	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.20	0.00
357850	5	0	3	0.00	152.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.20	0.10	0.00
357850	10	0	1	0.00	0.00	8.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
357850	10	0	2	1.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
357850	10	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
357850	20	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
357850	20	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
357850	20	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix A

MERCATOR COORDINATES	Dist. (M)	SHORE	QUADRAT (X OF 3)		E.can. (g/m2)	P. rich. (g/m2)	M. exalb. (g/m2)	C. dem. (g/m2)	R. aquat (g/m2)	P. pect. (g/m2)	P. gram. (g/m2)	S. cun. (g/m2)	C. herm. (g/m2)	P. berch. (g/m2)	L. aquat. (g/m2)	Chara (g/m2)	Mosses (g/m2)	Misc. (g/m2)
357850	5	1		1	39.76	542.47	119.87	3.26	0.00	0.00	0.00	0.00	0.00	0.79	0.00	0.10	0.00	71.80
357850	5	1		2	198.00	222.72	60.92	0.20	1.09	0.00	0.00	0.00	0.00	5.04	0.00	0.69	0.16	68.04
357850	5	1		3	143.80	166.84	45.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	132.53
357850	10	1		1	486.49	5.14	184.35	0.00	2.18	0.00	0.00	0.00	0.20	7.62	0.00	1.09	0.49	31.75
357850	10	1		2	78.13	51.13	261.29	0.00	0.00	0.00	0.00	0.00	0.00	2.27	0.00	0.00	0.00	21.07
357850	10	1		3	373.55	0.30	263.57	0.00	1.29	0.00	0.00	0.00	0.00	2.27	0.00	1.09	0.59	34.71
357850	20	1		1	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
357850	20	1		2	2.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
357850	20	1		3	0.30	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
357850	30	1		1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
357850	30	1		2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
357850	30	1		3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
366857	5	0		1	0.10	0.49	0.10	0.00	0.69	9.10	1.68	0.00	0.00	0.10	0.00	0.00	0.00	2.08
366857	5	0		2	0.69	0.89	0.00	0.00	0.00	4.75	3.56	0.00	0.00	2.47	0.00	0.20	0.00	7.32
366857	5	0		3	6.43	2.77	0.00	0.00	0.00	1.68	10.29	0.00	0.00	10.88	0.00	0.20	0.00	8.31
366857	10	0		1	0.00	0.10	0.00	0.00	0.79	13.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
366857	10	0		2	9.10	5.93	0.00	0.00	0.59	0.89	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.20
366857	10	0		3	22.35	7.81	0.99	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.10	0.89
366857	15	0		1	0.00	0.00	0.00	0.00	3.86	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.49	0.00
366857	15	0		2	19.88	0.00	0.00	0.00	2.27	0.00	0.00	0.00	0.00	0.30	0.00	0.40	0.49	0.00
366857	15	0		3	142.12	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.59	0.00	0.49	0.10	2.27
366857	5	1		1	14.84	3.66	0.00	0.00	0.00	1.58	24.33	0.00	0.89	11.87	0.00	2.37	0.00	10.48
366857	5	1		2	11.77	14.84	0.20	0.00	0.00	0.00	26.70	0.00	1.58	15.43	0.10	2.47	0.00	10.98
366857	5	1		3	27.00	18.79	7.02	0.00	0.00	0.00	46.58	0.00	2.67	15.63	0.59	3.76	0.00	26.31
366857	10	1		1	71.70	11.47	3.07	0.00	0.00	0.00	2.47	0.00	0.00	0.20	0.00	0.30	0.00	4.55
366857	10	1		2	121.25	28.68	11.67	0.00	0.00	0.00	16.32	0.00	0.40	23.24	0.00	0.99	0.00	16.62
366857	10	1		3	198.29	31.15	16.42	0.00	0.00	0.00	17.31	0.00	1.48	37.58	0.00	2.67	0.00	20.18
366857	15	1		1	245.27	2.47	1.19	0.00	0.99	0.00	0.00	0.00	0.00	1.78	0.00	0.49	0.00	14.64
366857	15	1		2	254.96	48.66	8.51	0.00	0.00	0.00	0.00	0.00	0.00	3.56	0.00	6.13	0.00	34.32
366857	15	1		3	469.48	56.77	3.76	0.00	0.00	0.00	0.00	0.00	0.00	25.02	0.00	7.91	0.00	34.91
366857	20	1		1	142.51	18.10	82.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	45.99

Appendix A

MERCATOR COORDINATES	Dist. (M)	SHORE	QUADRAT (X OF 3)	E.can. (g/m2)	P. rich. (g/m2)	M. exalb. (g/m2)	C. dem. (g/m2)	R. aquat (g/m2)	P. pect. (g/m2)	P. gram. (g/m2)	S. cun. (g/m2)	C. herm. (g/m2)	P. berch. (g/m2)	L. aquat. (g/m2)	Chara (g/m2)	Moses (g/m2)	Misc. (g/m2)
366857	20	1	2	109.88	22.25	20.67	1.98	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.10	0.00	0.00
366857	20	1	3	219.46	35.31	62.50	3.66	0.59	0.00	0.00	0.00	0.00	0.30	0.00	0.69	0.20	19.38
366857	25	1	1	0.99	51.03	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
366857	25	1	2	15.03	43.02	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
366857	25	1	3	3.16	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00
366857	30	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
366857	30	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
366857	30	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
366857	35	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
366857	35	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
366857	35	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
382855	5	0	1	63.20	33.53	89.80	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.14
382855	5	0	2	23.24	130.15	89.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
382855	5	0	3	135.00	0.00	65.18	0.00	0.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00
382855	15	0	1	3.86	0.00	0.00	0.00	29.97	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.20
382855	15	0	2	0.00	0.00	0.00	0.00	9.79	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00
382855	15	0	3	10.29	0.00	0.00	0.00	46.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
382855	25	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
382855	25	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
382855	25	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
382855	10	1	1	43.61	1.58	0.00	1.78	0.10	0.00	52.02	0.00	0.20	0.79	0.00	1.29	0.10	18.99
382855	10	1	2	76.65	0.00	4.95	0.00	0.59	0.00	18.10	0.00	0.00	0.00	0.00	5.14	0.00	31.25
382855	10	1	3	90.00	0.00	2.77	16.71	0.30	0.00	51.13	0.00	0.10	1.88	0.00	10.58	0.00	36.59
382855	20	1	1	64.29	0.00	3.56	5.14	14.24	0.00	0.00	0.00	0.00	0.30	0.00	3.46	0.40	10.98
382855	20	1	2	56.08	10.58	61.61	0.00	3.26	0.00	0.00	0.00	0.00	1.48	0.00	1.09	0.00	19.48
382855	20	1	3	84.16	0.00	36.79	0.00	1.78	0.00	0.00	0.00	0.00	1.48	0.00	0.20	0.00	7.52
382855	30	1	1	198.49	0.00	11.77	0.00	2.57	0.00	0.00	0.00	0.00	0.10	0.00	1.68	0.10	7.42
382855	30	1	2	167.54	0.00	60.13	5.14	0.30	0.00	0.20	0.00	0.00	0.00	0.00	0.49	0.30	21.36
382855	30	1	3	322.51	0.89	17.11	0.10	1.19	0.00	0.10	0.00	0.10	0.99	0.00	2.27	0.40	0.00
382855	40	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
382855	40	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix A

MERCATOR COORDINATES	Dist. (M)	SHORE	QUADRAT (X OF 3)	E.can. (g/m2)	P. rich. (g/m2)	M. exalb. (g/m2)	C. dem. (g/m2)	R. aquat (g/m2)	P. pect. (g/m2)	P. gram. (g/m2)	S. can. (g/m2)	C. herm. (g/m2)	P. berch. (g/m2)	L. aquat. (g/m2)	Chara (g/m2)	Mosses (g/m2)	Misc. (g/m2)
382855	40	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
576806	5	0	1	16.52	9.59	0.00	0.00	4.25	0.00	0.10	0.00	0.10	3.26	0.00	0.00	0.00	3.16
576806	5	0	2	25.81	5.74	0.69	0.00	3.66	0.00	0.00	0.00	0.00	8.60	0.00	0.10	0.10	3.66
576806	5	0	3	1.29	36.00	0.00	0.00	0.20	0.00	3.76	0.00	0.00	0.30	0.00	0.00	0.00	0.99
576806	10	0	1	0.00	12.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.49
576806	10	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
576806	10	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
576806	15	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
576806	15	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
576806	15	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
576806	5	1	1	62.41	0.79	0.00	0.00	0.00	0.00	10.29	0.00	33.43	6.43	0.59	1.19	0.00	21.96
576806	5	1	2	0.00	6.82	0.00	0.00	0.00	0.00	15.53	40.35	0.00	8.90	1.38	2.57	0.00	25.32
576806	5	1	3	0.99	51.33	0.00	0.00	0.00	0.30	2.37	0.00	34.12	3.76	1.29	1.58	0.00	14.14
576806	10	1	1	138.16	42.03	0.00	0.00	0.00	1.48	6.82	0.00	39.07	81.30	0.00	0.40	0.00	27.40
576806	10	1	2	0.00	0.00	0.00	0.00	1.88	0.99	11.57	0.00	63.00	90.99	0.00	0.00	0.00	26.21
576806	10	1	3	25.81	23.34	1.38	0.00	0.40	0.00	0.00	0.00	32.34	66.36	0.10	0.10	0.00	27.10
576806	15	1	1	20.57	35.70	0.00	0.00	13.94	0.00	0.00	0.00	0.20	153.20	0.00	0.00	0.00	17.80
576806	15	1	2	18.99	61.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	184.84	0.00	0.00	0.00	23.24
576806	15	1	3	36.69	22.55	0.00	0.00	0.79	0.00	0.00	0.00	19.98	81.00	0.20	0.10	0.00	8.51
576806	20	1	1	1228.44	4.55	3.26	6.63	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00
576806	20	1	2	1547.98	10.29	14.64	13.55	0.10	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	54.79
576806	20	1	3	1120.54	0.00	4.15	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.00	0.00	0.00	46.98
576806	25	1	1	630.09	0.00	16.71	243.29	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	15.33
576806	25	1	2	1031.13	0.00	5.74	258.13	0.30	0.00	0.00	0.00	0.20	1.88	0.00	0.00	0.00	65.87
576806	25	1	3	485.30	10.38	3.66	167.24	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	57.26
576806	30	1	1	852.22	0.00	3.76	70.71	0.10	0.00	0.00	0.00	0.00	3.86	0.00	0.10	0.00	23.93
576806	30	1	2	832.44	0.00	3.16	57.96	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.00	28.09
576806	30	1	3	835.31	0.00	2.18	162.89	0.00	0.00	0.00	0.00	0.00	0.79	0.00	0.00	0.00	62.01
576806	35	1	1	1236.25	8.51	42.13	19.88	0.00	0.00	0.00	0.00	0.00	4.65	0.00	0.10	0.00	0.00
576806	35	1	2	1752.11	17.21	15.43	74.97	0.20	0.00	0.00	0.00	0.10	1.58	0.00	0.00	0.00	6.33
576806	35	1	3	797.04	42.53	8.01	47.77	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00

Appendix A

MERCATOR COORDINATES	Dist. (M)	SHORE	QUADRAT (X OF 3)	E.can. (g/m2)	P. rich. (g/m2)	M. exalb. (g/m2)	C. dem. (g/m2)	R. aquat (g/m2)	P. pect. (g/m2)	P. gram. (g/m2)	S. can. (g/m2)	C. herm. (g/m2)	P. berch. (g/m2)	L. aquat. (g/m2)	Chara (g/m2)	Mosses (g/m2)	Misc. (g/m2)
576806	40	1	1	28.09	43.61	0.00	0.49	0.00	0.00	0.00	0.00	0.00	0.30	0.00	0.00	0.00	4.15
576806	40	1	2	27.30	57.46	1.88	19.38	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.51
576806	40	1	3	7.91	80.50	0.00	4.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.18
576806	45	1	1	16.71	147.46	26.11	2.57	0.00	0.00	0.00	0.00	0.00	0.79	0.00	0.00	0.00	0.00
576806	45	1	2	63.39	440.70	2.27	14.14	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	17.51
576806	45	1	3	5.74	112.55	17.60	16.32	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	9.10
576806	50	1	1	121.65	32.34	2.47	5.93	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	14.84
576806	50	1	2	823.64	96.72	15.63	4.35	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	57.26
576806	50	1	3	433.87	90.39	7.22	3.56	0.40	0.00	0.00	0.00	0.00	0.30	0.00	0.00	0.00	32.04
576806	55	1	1	54.99	77.64	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	32.93
576806	55	1	2	301.55	277.41	37.88	34.42	0.00	0.00	0.00	0.00	0.00	4.75	0.00	0.00	0.00	118.78
576806	55	1	3	9.99	75.76	9.79	9.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
576806	60	1	1	297.79	4.85	0.89	0.10	0.10	0.00	0.00	0.00	0.00	0.30	0.00	0.10	0.00	13.25
576806	60	1	2	638.80	27.00	20.47	18.20	0.20	0.00	0.00	0.00	0.00	0.49	0.00	0.00	0.00	26.51
576806	60	1	3	116.90	11.37	27.79	12.46	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	23.44
576806	65	1	1	0.00	74.37	0.00	0.00	0.30	0.00	0.00	0.00	0.00	7.52	0.00	0.10	0.00	9.30
576806	65	1	2	119.37	50.14	23.74	66.07	0.10	0.00	1.19	0.00	0.00	123.72	0.00	0.10	0.00	42.82
576806	65	1	3	8.01	90.10	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.59	0.00	0.00	0.00	7.81
576806	70	1	1	0.00	10.78	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.10	0.10	0.00
576806	70	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
576806	70	1	3	0.20	7.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
576806	75	1	1	0.00	0.00	2.87	0.00	0.00	0.00	0.00	0.00	0.00	0.59	0.00	0.00	0.00	0.59
576806	75	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00
576806	75	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
576806	80	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
576806	80	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
576806	80	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
601819	5	0	1	0.79	0.00	0.00	0.00	2.57	0.00	9.30	0.00	0.79	0.00	2.77	0.69	0.00	2.37
601819	5	0	2	0.00	0.00	0.00	0.00	0.00	0.00	7.81	0.00	0.00	0.10	10.19	1.68	0.00	1.68
601819	5	0	3	1.68	14.84	0.00	0.00	0.30	0.00	9.40	0.10	0.00	1.78	4.05	0.20	0.30	4.75
601819	10	0	1	382.45	59.93	0.59	0.00	0.00	0.00	19.38	0.00	0.00	0.00	0.00	0.00	0.00	0.40

Appendix A

MERCATOR COORDINATES	Dist. (M)	SHORE	QUADRAT (X OF 3)	E.can. (g/m2)	P. rich. (g/m2)	M. exalb. (g/m2)	C. dem. (g/m2)	R. aquat (g/m2)	P. pect. (g/m2)	P. gram. (g/m2)	S. cun. (g/m2)	C. herm. (g/m2)	P. berch. (g/m2)	L. aquat. (g/m2)	Chara (g/m2)	Mosses (g/m2)	Misc. (g/m2)
601819	10	0	2	0.00	145.68	0.00	0.00	0.10	0.00	2.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00
601819	10	0	3	0.00	59.54	0.00	0.00	0.00	0.00	9.59	0.00	0.00	0.00	0.49	0.00	0.00	0.00
601819	15	0	1	0.69	23.34	0.00	0.00	258.72	0.00	8.51	0.00	0.00	0.30	0.00	0.00	0.49	10.98
601819	15	0	2	0.00	1.29	0.00	0.00	7.91	0.00	0.00	0.00	0.00	0.30	0.20	0.00	0.20	2.27
601819	15	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
601819	20	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
601819	20	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
601819	20	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
601819	5	1	1	0.99	0.00	0.00	0.00	3.66	0.00	4.85	0.00	0.00	0.10	0.59	0.00	0.00	1.98
601819	5	1	2	1.38	0.00	0.00	0.00	4.45	0.00	0.00	0.00	0.00	0.00	2.08	0.00	0.10	0.79
601819	5	1	3	0.00	0.00	0.10	0.00	19.78	0.00	1.48	0.00	0.00	0.59	3.66	0.40	0.00	4.55
601819	10	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
601819	10	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
601819	10	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
846788	5	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
846788	5	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
846788	5	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
846788	10	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	43.81	0.00
846788	10	1	2	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.04	0.00	0.00	0.00	157.35	0.00
846788	10	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	141.03	0.00
846788	15	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
846788	15	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
846788	15	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
973912	5	0	1	12.86	2.87	0.00	0.00	0.00	15.53	0.00	0.00	16.02	64.38	0.69	3.66	0.10	33.63
973912	5	0	2	7.91	0.00	0.00	1.58	0.00	3.66	0.00	0.00	5.34	110.57	0.10	0.89	0.00	0.69
973912	5	0	3	22.35	42.03	0.00	0.00	0.00	3.96	0.00	0.00	2.57	41.54	0.10	1.68	0.20	9.69
973912	10	0	1	111.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.88	20.77	0.00	3.07	0.00	19.29
973912	10	0	2	87.82	0.89	0.00	0.00	0.20	0.00	0.00	0.00	1.29	38.37	0.00	4.75	0.10	27.79
973912	10	0	3	114.13	0.00	0.00	0.00	0.20	0.00	0.00	0.00	1.38	69.63	0.00	14.93	0.30	37.48
973912	15	0	1	404.50	18.10	13.55	0.00	0.59	0.00	0.00	0.00	0.20	0.69	0.00	2.37	0.10	16.81
973912	15	0	2	117.99	23.64	7.52	0.00	0.10	0.00	0.00	0.00	0.20	0.30	0.00	1.48	0.10	10.38

Appendix A

MERCATOR COORDINATES	Dist. (M)	SHORE	QUADRAT (X OF 3)	E.can. (g/m2)	P. rich. (g/m2)	M. exalb. (g/m2)	C. dem. (g/m2)	R. aquat (g/m2)	P. pect. (g/m2)	P. gram. (g/m2)	S. cun. (g/m2)	C. herm. (g/m2)	P. berch. (g/m2)	L. aquat. (g/m2)	Chara (g/m2)	Mosses (g/m2)	Misc. (g/m2)
973912	15	0	3	173.47	13.65	16.71	0.00	0.20	0.00	0.00	0.00	0.49	20.87	0.00	2.47	0.10	16.71
973912	20	0	1	172.78	6.73	13.85	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00	4.05
973912	20	0	2	639.19	9.79	4.95	0.00	1.58	0.00	0.00	0.00	0.10	2.47	0.00	2.47	0.20	4.05
973912	20	0	3	173.27	24.53	12.07	0.00	0.00	0.00	0.00	0.00	0.20	6.43	0.00	1.58	0.10	0.00
973912	25	0	1	581.43	54.59	11.47	0.00	3.36	0.00	0.00	0.00	0.00	2.77	0.00	1.38	0.69	21.56
973912	25	0	2	363.95	9.79	2.08	0.00	0.20	0.00	0.00	0.00	0.00	0.49	0.00	0.30	0.20	2.77
973912	25	0	3	301.05	17.60	6.82	0.00	5.54	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.20	13.65
973912	30	0	1	230.34	5.74	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10	0.00
973912	30	0	2	272.87	4.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00	2.47
973912	30	0	3	625.64	81.30	0.00	0.00	0.49	0.00	0.00	0.00	0.00	2.08	0.00	2.77	2.47	39.36
973912	35	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
973912	35	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
973912	35	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
973912	5	1	1	24.92	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00
973912	5	1	2	1054.57	0.00	0.10	0.00	0.30	0.00	0.00	0.00	0.00	0.69	0.00	0.40	0.20	0.00
973912	5	1	3	798.72	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.20	0.10	0.00
973912	10	1	1	312.62	0.00	0.00	0.00	2.97	0.00	0.00	0.00	0.00	0.20	0.00	1.09	0.10	0.00
973912	10	1	2	66.66	0.59	0.10	0.00	4.35	0.00	0.00	0.00	0.00	20.27	0.00	1.88	0.20	24.03
973912	10	1	3	208.38	0.00	0.00	0.00	0.40	0.40	0.00	0.00	0.00	0.30	0.00	0.59	0.00	0.00
973912	15	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.09	0.00	0.69
973912	15	1	2	360.99	0.00	0.00	0.00	0.59	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00
973912	15	1	3	801.49	0.00	0.10	0.00	0.69	0.00	0.00	0.00	0.00	0.30	0.00	0.79	0.10	0.00
973912	20	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
973912	20	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
973912	20	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
984905	5	0	1	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.10	0.00	0.10	0.00	0.00
984905	5	0	2	24.03	0.00	37.19	0.00	0.69	0.00	1.68	0.00	0.00	0.00	0.00	1.19	0.00	11.67
984905	5	0	3	31.15	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.00	0.59	0.00	0.00
984905	10	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
984905	10	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
984905	10	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix A

MERCATOR COORDINATES	Dist. (M)	SHORE	QUADRAT (X OF 3)	E.can. (g/m2)	P. rich. (g/m2)	M. exalb. (g/m2)	C. dem. (g/m2)	R. aquat. (g/m2)	P. pect. (g/m2)	P. gram. (g/m2)	S. can. (g/m2)	C. herm. (g/m2)	P. berch. (g/m2)	L. aquat. (g/m2)	Chara (g/m2)	Mosses (g/m2)	Misc. (g/m2)
984905	15	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
984905	15	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
984905	15	0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
984905	5	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.60	1.88	0.00	2.97	0.20	4.35
984905	5	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.67	0.99	0.00	2.08	0.10	14.24
984905	5	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	32.34	6.82	0.00	8.01	0.00	18.20
984905	10	1	1	0.00	12.66	0.00	0.00	0.00	1.09	0.00	0.00	15.92	28.68	0.00	3.66	0.99	18.10
984905	10	1	2	0.00	1.09	0.00	0.00	0.00	0.49	0.00	0.00	20.47	49.75	0.00	10.88	0.59	34.02
984905	10	1	3	0.10	2.18	0.10	0.00	0.00	0.69	0.00	0.00	2.67	5.74	0.00	7.62	0.89	0.00
984905	15	1	1	1.68	3.56	0.00	0.00	0.00	5.74	0.00	0.00	7.52	72.69	0.30	3.16	0.49	1.38
984905	15	1	2	0.00	0.49	0.00	0.00	0.49	0.00	0.00	0.00	17.90	79.42	0.20	2.18	0.99	22.75
984905	15	1	3	0.00	1.38	0.00	0.00	6.03	4.15	0.00	0.00	27.69	82.28	0.40	1.19	3.07	56.08
984905	20	1	1	0.00	0.00	0.00	0.00	0.00	7.91	0.00	0.00	7.52	34.22	0.20	1.98	0.30	9.59
984905	20	1	2	0.00	0.00	1.29	0.00	0.00	0.89	0.00	0.00	5.04	2.97	2.47	3.96	0.49	16.42
984905	20	1	3	0.00	5.34	0.00	0.00	0.00	3.46	0.00	0.00	9.89	13.35	6.43	1.88	0.40	23.14
984905	25	1	1	0.00	25.42	0.00	0.00	0.00	0.00	0.00	0.00	12.76	46.48	0.00	3.86	6.43	0.00
984905	25	1	2	0.00	36.49	0.00	0.00	0.40	0.00	0.00	0.00	3.26	43.02	0.00	0.69	0.30	4.35
984905	25	1	3	0.30	74.97	0.00	0.00	16.22	0.00	0.00	0.00	1.48	12.36	0.00	0.79	0.99	7.32
984905	30	1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
984905	30	1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
984905	30	1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

APPENDIX B: Physical and chemical conditions associated with aquatic macrophytes for sites in the Nechako River, British Columbia

Legend:

1. Merc coord = Universal transverse mercator grid coordinate as read from 1:50000 map (location of site)
2. Dist. = distance from shore sample collected from (m)
3. Quad. = n of 3 replicates taken at each sampling interval
4. Depth = depth of sampling interval on day of collection
5. Velocity = average current speed of sampling interval on day of collection
6. Exch. P. = Exchangeable phosphorus concentration of sediments at sampling interval (mean of 2)
7. Exch. N. = Exchangeable nitrogen concentration of sediments at sampling interval (mean of 2)
8. Phi = the negative logarithm in base 2 of the particle size in mm (the number associated with the phi scale is the proportion, by mass, of the total sediment sample falling within the phi range)

Appendix B

Merc coord	Dist. (m)	Shore	Quad	Depth (m)	velocity (m3/s)	Exch. P (ug/g)	Exch. N (ug/g)	phi -2	phi -1.5	phi -1	phi -0.5	phi 0	phi 0.5	phi 1	phi 1.5	phi 2	phi 2.5	phi 3	phi 3.5	phi 4	phi 4.5	phi 5	phi 5.5	phi 6	phi 6.5	phi 7	phi 7.5	phi 8	phi 8.5	phi 9	phi 9.5	phi 10	phi 10.5
36728	5	0	2	0.3	0.00	490.0	38.8	0	0	0	0	0.01	0.01	0.22	0.45	2.16	4.63	15.3	15.2	15.9	11.8	7.83	4.54	6.08	4.1	3.2	2.74	2.39	1.88	1.1	0.25	0.17	0
36728	5	0	3	0.3	0.00	425.0	22.1	0	0	0	0	0	0	0.18	0.66	3.15	9.43	20.2	22.5	14.6	10.8	6.58	2.47	4.08	1.17	1.16	0.82	0.58	0.41	0.29	0.21	0.15	0
36728	10	0	1	0.3	0.00	550.0	10.6	0	0	0	0	0	0	0.01	0.89	7.3	10.1	23.6	19.3	11.6	8.04	4.42	2.09	3.85	2.93	1.61	1.38	1.27	1	0.58	0.11	0.07	0
36728	10	0	2	0.3	0.00	527.7	5.7	0	0	0	0	0.02	0.01	0.53	2.74	9.79	19.6	21.2	15.7	10.8	5.78	3.44	1.89	3.26	1.65	1.13	0.8	0.57	0.4	0.28	0.2	0.14	0
36728	10	0	3	0.3	0.00	519.8	10.4																										.
36728	15	0	1	0.5	0.42	234.0	6.7	0	0	0	0.15	0.69	0.49	6.95	14	21.4	19.4	11.9	8.62	5.28	2.38	1.48	0.99	2.28	1.28	0.89	0.63	0.44	0.31	0.22	0.16	0.11	0
36728	15	0	2	0.5	0.42	295.0	20.3	0	0	0	0.3	1.39	1.04	8.27	12.4	15.5	7.19	10.5	9.85	10.5	5.61	2.96	2.36	3.09	1.94	1.74	1.64	1.5	1.22	0.73	0.18	0.12	0
36728	15	0	3	0.5	0.42	194.0	5.4																										.
36728	20	0	1	0.8	0.54	0.0	0.0																										.
36728	20	0	2	0.8	0.54	0.0	0.0																										.
36728	20	0	3	0.8	0.54	0.0	0.0																										.
36728	5	1	1	0.8	1.07	0.0	0.0																										.
36728	5	1	2	0.8	1.07	0.0	0.0																										.
36728	5	1	3	0.8	1.07	0.0	0.0																										.
39752	5	0	1	0.3	0.42	188.0	5.2																										.
39752	5	0	2	0.3	0.42																												.
39752	5	0	3	0.3	0.42																												.
39752	5	1	1	0.6	0.56	114.0	9.0																										.
39752	5	1	2	0.6	0.56																												.
39752	5	1	3	0.6	0.56																												.
124773	5	0	1	0.9	0.13																												.
124773	5	0	2	0.9	0.13																												.
124773	5	0	3	0.9	0.13																												.
124773	10	0	1	2.5	0.11	487.6	23.7	0	0	0	0.01	0.03	0.02	0.86	2.15	5.99	8.97	18.3	14.6	12.2	8.85	6.78	4.69	5.14	2.96	2.4	2.03	1.73	1.31	0.74	0.16	0.11	0
124773	10	0	2	2.5	0.11	364.4	19.5	0	0	0	0.01	0.03	0.02	1	3.24	10.1	12.5	19.6	13.6	9.02	6.88	5.44	4.01	4.51	2.62	2.15	1.81	1.54	1.16	0.62	0.14	0.09	0
124773	10	0	3	2.5	0.11																												.
124773	15	0	1	3.4	0.43																												.
124773	15	0	2	3.4	0.43																												.
124773	15	0	3	3.4	0.43																												.
124773	5	1	1	0.9	0.14																												.
124773	5	1	2	0.9	0.14																												.

Appendix B

Merc coord	Dist. (m)	Shore	Quad	Depth (m)	velocity (m3/s)	Exch. P (ug/g)	Exch. N (ug/g)	phi -2	phi -1.5	phi -1	phi -0.5	phi 0	phi 0.5	phi 1	phi 1.5	phi 2	phi 2.5	phi 3	phi 3.5	phi 4	phi 4.5	phi 5	phi 5.5	phi 6	phi 6.5	phi 7	phi 7.5	phi 8	phi 8.5	phi 9	phi 9.5	phi 10	phi 10.5
27760	5	0	1	1.1	0.70	0.0	0.0																										.
27760	5	0	2	1.1	0.70	0.0	0.0																										.
27760	5	0	3	1.1	0.70	0.0	0.0																										.
27760	10	0	1	1.3	0.85	0.0	0.0																										.
27760	10	0	2	1.3	0.85	0.0	0.0																										.
27760	10	0	3	1.3	0.85	0.0	0.0																										.
27760	5	1	1	1.0	1.04	0.0	0.0																										.
27760	5	1	2	1.0	1.04	0.0	0.0																										.
27760	5	1	3	1.0	1.04	0.0	0.0																										.
27760	10	1	1	2.0	1.58	0.0	0.0																										.
27760	10	1	2	2.0	1.58	0.0	0.0																										.
27760	10	1	3	2.0	1.58	0.0	0.0																										.
27772	5	0	1	0.8	0.92	0.0	0.0																										.
27772	5	0	2	0.8	0.92	0.0	0.0																										.
27772	5	0	3	0.8	0.92	0.0	0.0																										.
27772	10	0	1	1.0	1.15	0.0	0.0																										.
27772	10	0	2	1.0	1.15	0.0	0.0																										.
27772	10	0	3	1.0	1.15	0.0	0.0																										.
27772	5	1	1	1.4	0.92	0.0	0.0																										.
27772	5	1	2	1.4	0.92	0.0	0.0																										.
27772	5	1	3	1.4	0.92	0.0	0.0																										.
27772	10	1	1	1.9	0.94	0.0	0.0																										.
27772	10	1	2	1.9	0.94	0.0	0.0																										.
27772	10	1	3	1.9	0.94	0.0	0.0																										.
29745	5	0	1	0.3	0.19	0.0	0.0																										.
29745	5	0	2	0.3	0.19	0.0	0.0																										.
29745	5	0	3	0.3	0.19	0.0	0.0																										.
29745	5	1	1	0.5	0.28	0.0	0.0																										.
29745	5	1	2	0.5	0.28	0.0	0.0																										.
29745	5	1	3	0.5	0.28	0.0	0.0																										.
36728	5	0	1	0.3	0.00	452.0	30.4	0	0	0	0	0	0	0.05	0.26	2.05	5.19	16.7	15.8	15	10.8	7.21	4.34	6.01	4.14	3.41	2.93	2.53	1.99	1.18	0.27	0.18	0

Appendix B

Mere coord	Dist. (m)	Shore	Quad	Depth (m)	velocity (m3/s)	Exch. P (ug/g)	Exch. N (ug/g)	phi -2	phi -1.5	phi -1	phi -0.5	phi 0	phi 0.5	phi 1	phi 1.5	phi 2	phi 2.5	phi 3	phi 3.5	phi 4	phi 4.5	phi 5	phi 5.5	phi 6	phi 6.5	phi 7	phi 7.5	phi 8	phi 8.5	phi 9	phi 9.5	phi 10	phi 10.5
124773	5	1	3	0.9	0.14																												.
124773	10	1	1	1.6	0.74	0.0	0.0																										.
124773	10	1	2	1.6	0.74	0.0	0.0																										.
124773	10	1	3	1.6	0.74	0.0	0.0																										.
124773	15	1	1	2.0	0.98	0.0	0.0																										.
124773	15	1	2	2.0	0.98	0.0	0.0																										.
124773	15	1	3	2.0	0.98	0.0	0.0																										.
144773	5	0	1	1.2	0.58																												.
144773	5	0	2	1.2	0.58																												.
144773	5	0	3	1.2	0.58																												.
144773	10	0	1	2.3	0.87	0.0	0.0																										.
144773	10	0	2	2.3	0.87	0.0	0.0																										.
144773	10	0	3	2.3	0.87	0.0	0.0																										.
144773	5	1	1	0.9	0.69	0.0	0.0																										.
144773	5	1	2	0.9	0.69	0.0	0.0																										.
144773	5	1	3	0.9	0.69	0.0	0.0																										.
144773	10	1	1	1.3	0.95	0.0	0.0																										.
144773	10	1	2	1.3	0.95	0.0	0.0																										.
144773	10	1	3	1.3	0.95	0.0	0.0																										.
153911	5	0	1	0.9	0.71	0.0	0.0																										.
153911	5	0	2	0.9	0.71	0.0	0.0																										.
153911	5	0	3	0.9	0.71	0.0	0.0																										.
153911	5	1	1	0.3	0.51																												.
153911	5	1	2	0.3	0.51																												.
153911	5	1	3	0.3	0.51																												.
157912	5	0	1	0.6	0.09																												.
157912	5	0	2	0.6	0.09																												.
157912	5	0	3	0.6	0.09																												.
157912	10	0	1	0.8	0.54																												.
157912	10	0	2	0.8	0.54																												.
157912	10	0	3	0.8	0.54																												.

Appendix B

Merc coord	Dist. (m)	Shore	Quad	Depth (m)	velocity (m3/s)	Exch. P (ug/g)	Exch. N (ug/g)	phi -2	phi -1.5	phi -1	phi -0.5	phi 0	phi 0.5	phi 1	phi 1.5	phi 2	phi 2.5	phi 3	phi 3.5	phi 4	phi 4.5	phi 5	phi 5.5	phi 6	phi 6.5	phi 7	phi 7.5	phi 8	phi 8.5	phi 9	phi 9.5	phi 10	phi 10.5
157912	5	1	1	0.4	0.37																												.
157912	5	1	2	0.4	0.37																												.
157912	5	1	3	0.4	0.37																												.
161912	5	0	1	0.1	0.15																												.
161912	5	0	2	0.1	0.15																												.
161912	5	0	3	0.1	0.15																												.
161912	5	1	1	0.4	0.09																												.
161912	5	1	2	0.4	0.09																												.
161912	5	1	3	0.4	0.09																												.
165910	5	0	1	0.9	0.63	0.0	0.0																										.
165910	5	0	2	0.9	0.63	0.0	0.0																										.
165910	5	0	3	0.9	0.63	0.0	0.0																										.
165910	5	1	1	0.3	0.24																												.
165910	5	1	2	0.3	0.24																												.
165910	5	1	3	0.3	0.24																												.
269891	5	0	1	0.4	0.52																												.
269891	5	0	2	0.4	0.52																												.
269891	5	0	3	0.4	0.52																												.
269891	5	1	1	0.7	0.46																												.
269891	5	1	2	0.7	0.46																												.
269891	5	1	3	0.7	0.46																												.
315859	5	0	1	0.2	0.32																												.
315859	5	0	2	0.2	0.32																												.
315859	5	0	3	0.2	0.32																												.
315859	10	0	1	0.8	0.01																												.
315859	10	0	2	0.8	0.01																												.
315859	10	0	3	0.8	0.01																												.
315859	5	1	1	0.3	0.04																												.
315859	5	1	2	0.3	0.04																												.
315859	5	1	3	0.3	0.04																												.
315859	10	1	1	0.3	0.01	0.0	0.0																										.

Appendix B

Merc coord	Dist. (m)	Shore	Quad	Depth (m)	velocity (m3/s)	Exch. P (ug/g)	Exch. N (ug/g)	phi -2	phi -1.5	phi -1	phi -0.5	phi 0	phi 0.5	phi 1	phi 1.5	phi 2	phi 2.5	phi 3	phi 3.5	phi 4	phi 4.5	phi 5	phi 5.5	phi 6	phi 6.5	phi 7	phi 7.5	phi 8	phi 8.5	phi 9	phi 9.5	phi 10	phi 10.5
315859	10	1	2	0.3	0.01	0.0	0.0																										.
315859	10	1	3	0.3	0.01	0.0	0.0																										.
315859	15	1	1	0.3	0.06																												.
315859	15	1	2	0.3	0.06																												.
315859	15	1	3	0.3	0.06																												.
337867	5	0	1	0.6	0.01																												.
337867	5	0	2	0.6	0.01																												.
337867	5	0	3	0.6	0.01																												.
337867	10	0	1	0.3	0.19	173.0	3.2	0	0	0	1.36	6.3	4.86	27.2	23.2	18.6	7.88	3.89	2.29	0.69	0.64	0.39	0.36	0.81	0.5	0.35	0.25	0.17	0.12	0.09	0.06	0.04	0
337867	10	0	2	0.3	0.19	110.6	2.5																										.
337867	10	0	3	0.3	0.19	158.1	7.2	0	0	0	4.48	20.7	22.1	26.6	11.9	7.23	3.3	0.53	1.15	0.12	0.36	0.17	0.11	0.33	0.3	0.21	0.15	0.11	0.08	0.05	0.04	0.03	0
337867	5	1	1	1.5	0.53																												.
337867	5	1	2	1.5	0.53																												.
337867	5	1	3	1.5	0.53																												.
344863	10	0	1	0.3	0.24	180.4	4.6	0	0	0	1.88	8.66	6.95	23.3	18.6	16.1	10.3	5.57	3.29	1.44	0.94	0.43	0.37	0.85	0.44	0.31	0.22	0.15	0.11	0.08	0.05	0.04	0
344863	10	0	2	0.3	0.24	180.0	6.0																										.
344863	10	0	3	0.3	0.24	213.3	7.9	0	0	0	2.16	9.95	8.17	29.1	20.7	14.7	6.66	2.69	1.94	0.73	0.7	0.37	0.28	0.58	0.39	0.27	0.19	0.14	0.1	0.07	0.05	0.03	0
344863	20	0	1	0.8	0.24	192.3	5.3	0	0	0	1.01	4.68	3.53	16.7	19.2	22.4	15.7	7.36	3.77	1.8	0.76	0.56	0.31	0.69	0.45	0.31	0.22	0.16	0.11	0.08	0.06	0.04	0
344863	20	0	2	0.8	0.24	224.8	3.2																										.
344863	20	0	3	0.8	0.24	183.7	6.6																										.
344863	30	0	1	1.2	0.66	184.9	2.7																										.
344863	30	0	2	1.2	0.66																												.
344863	30	0	3	1.2	0.66																												.
344863	40	0	1	1.7	0.67	142.2	3.3	0	0	0	1.68	7.74	6.11	31.5	26.5	17.9	5.43	1.55	0.72	0.15	0.1	0.06	0.05	0.15	0.12	0.08	0.06	0.04	0.03	0.02	0.01	0.01	0
344863	40	0	2	1.7	0.67																												.
344863	40	0	3	1.7	0.67																												.
344863	10	1	1	1.2	0.57	226.9	4.5																										.
344863	10	1	2	1.2	0.57	215.0	7.7																										.
344863	10	1	3	1.2	0.57	185.6	18.9	0	0	0	0.83	3.83	2.85	10.3	11.6	17.2	21.5	15	6.93	3.08	1.3	0.85	0.69	1.47	0.79	0.54	0.38	0.27	0.19	0.14	0.1	0.07	0
344863	20	1	1	1.9	0.77	0.0	0.0																										.
344863	20	1	2	1.9	0.77	0.0	0.0																										.

Appendix B

Merc coord	Dist. (m)	Shore	Quad	Depth (m)	velocity (m3/s)	Exch. P (ug/g)	Exch. N (ug/g)	phi -2	phi -1.5	phi -1	phi -0.5	phi 0	phi 0.5	phi 1	phi 1.5	phi 2	phi 2.5	phi 3	phi 3.5	phi 4	phi 4.5	phi 5	phi 5.5	phi 6	phi 6.5	phi 7	phi 7.5	phi 8	phi 8.5	phi 9	phi 9.5	phi 10	phi 10.5
344863	20	1	3	1.9	0.77	0.0	0.0																										.
356865	10	0	1	1.0	0.05	664.6	56.2	0	0	0	0	0	0	0	0	0	1.44	6.67	4.71	14.7	12.3	12.5	12.2	10.8	8.17	5.79	4.02	3.03	2.29	1.1	0.21	0.14	0
356865	10	0	2	1.0	0.05	639.5	53.1	0	0	0	0	0	0	0	0	0	1.64	7.59	5.37	15.1	12.1	11.9	11.8	10.4	7.87	5.63	3.39	3.03	2.22	1.1	0.22	0.15	0
356865	10	0	3	1.0	0.05	606.0	55.9	0	0	0	0	0	0	0	0	0	1.38	6.37	4.51	14.9	12.5	12.3	12.2	10.6	8.06	5.88	4.13	3.19	2.34	1.19	0.25	0.17	0
356865	20	0	1	2.0	0.35	171.8	4.5																										.
356865	20	0	2	2.0	0.35	205.8	6.1																										.
356865	20	0	3	2.0	0.35																												.
356865	30	0	1	3.0	0.52	192.3	6.2	0	0	0	1.45	6.68	5.18	27.2	27.4	21.2	6.47	1.93	1.39	0.25	0.09	0.07	0.05	0.15	0.14	0.1	0.07	0.05	0.03	0.02	0.02	0.01	0
356865	30	0	2	3.0	0.52																												.
356865	30	0	3	3.0	0.52																												.
356865	10	1	1	1.2	0.00	657.3	43.0	0	0	0	0	0	0	0	0	0	0.9	4.16	2.94	6.26	6.37	7.36	9.49	12.3	11.9	10.6	9.15	7.51	5.83	3.65	0.94	0.64	0.01
356865	10	1	2	1.2	0.00	700.0	37.2	0	0	0	0	0	0	0	0	0	0.9	4.18	2.95	5.26	6.28	8.79	10.6	11.9	12.2	10.4	8.78	7.18	5.42	3.51	0.95	0.64	0.01
356865	10	1	3	1.2	0.00	466.7	34.1	0	0	0	0	0	0	0.16	0.25	3.85	2.46	4.16	5.43	8.09	9.58	12.5	8.86	9.75	10.8	7.82	5.67	4.04	2.76	1.72	0.93	1.15	0.02
356865	20	1	1	3.3	0.03	488.3	37.7	0	0	0	0	0	0	1.65	8.29	15.7	9	8.07	5.49	3.49	4.33	5.33	4.19	6.94	7.13	5.61	4.65	3.75	2.87	1.94	0.84	0.71	0.01
356865	20	1	2	3.3	0.03	421.6	18.4																										.
356865	20	1	3	3.3	0.03	437.8	27.0	0	0	0	0.02	0.1	0.07	10.9	10.6	9.07	4.74	5.55	3.84	4.2	4.9	6.05	6.27	6.49	7.41	5.49	4.7	3.93	3.01	1.85	0.47	0.32	0.01
356865	30	1	1	3.8	0.19	204.8	6.7																										.
356865	30	1	2	3.8	0.19	246.4	6.5																										.
356865	30	1	3	3.8	0.19	233.8	5.8																										.
356865	40	1	1	4.2	0.42																												.
356865	40	1	2	4.2	0.42																												.
356865	40	1	3	4.2	0.42																												.
357850	5	0	1	1.6	0.17	218.0	22.7																										.
357850	5	0	2	1.6	0.17	332.0	36.6																										.
357850	5	0	3	1.6	0.17	272.0	26.5																										.
357850	10	0	1	2.9	0.30	190.1	3.6																										.
357850	10	0	2	2.9	0.30	264.4	12.8																										.
357850	10	0	3	2.9	0.30	179.8	10.9																										.
357850	20	0	1	3.6	0.37	325.0	8.5	0	0	0	0.73	3.39	2.51	13.3	14.1	17.9	18.1	11	6.05	2.77	1.41	1.42	0.97	2.25	1.29	0.89	0.63	0.45	0.32	0.22	0.16	0.11	0
357850	20	0	2	3.6	0.37	191.3	13.4																										.
357850	20	0	3	3.6	0.37																												.

Appendix B

Merc coord	Dist. (m)	Shore	Quad	Depth (m)	velocity (m3/s)	Exch. P (ug/g)	Exch. N (ug/g)	phi -2	phi -1.5	phi -1	phi -0.5	phi 0	phi 0.5	phi 1	phi 1.5	phi 2	phi 2.5	phi 3	phi 3.5	phi 4	phi 4.5	phi 5	phi 5.5	phi 6	phi 6.5	phi 7	phi 7.5	phi 8	phi 8.5	phi 9	phi 9.5	phi 10	phi 10.5
357850	5	1	1	0.6	0.00																												.
357850	5	1	2	0.6	0.00																												.
357850	5	1	3	0.6	0.00																												.
357850	10	1	1	1.0	0.00	495.6	54.4	0	0	0	0	0	0	0	0	0	1.47	6.81	4.81	10.8	10.9	12.5	12.3	11.3	9.32	6.53	4.92	3.79	2.62	1.39	0.31	0.21	0
357850	10	1	2	1.0	0.00	268.6	34.4																										.
357850	10	1	3	1.0	0.00	382.9	34.9	0	0	0	0.05	0.24	0.18	3.6	7.61	11.4	6.99	10.5	9.79	7.94	6.71	7.18	5.54	6.81	4.51	3.54	2.7	2.13	1.48	0.81	0.19	0.13	0
357850	20	1	1	2.6	0.20	417.2	42.1	0	0	0	0.06	0.27	0.19	2.37	5.86	14	23.3	19.1	10.8	5.66	3.13	3.27	2.65	3.96	1.71	1.17	0.83	0.59	0.41	0.29	0.21	0.15	0
357850	20	1	2	2.6	0.20	289.6	32.4																										.
357850	20	1	3	2.6	0.20	295.6	35.5																										.
357850	30	1	1	3.0	0.29	350.5	4.3	0	0	0	0.08	0.37	0.26	15.7	37.1	34.8	8.29	1.89	0.8	0.11	0.11	0.09	0.02	0.05	0.11	0.08	0.06	0.04	0.03	0.02	0.01	0.01	0
357850	30	1	2	3.0	0.29	274.3	2.7	0	0	0	0.15	0.68	0.48	17.6	37.2	33.8	7.54	1.44	0.63	0.07	0.05	0.05	0.01	0.05	0.07	0.05	0.03	0.02	0.02	0.01	0.01	0.01	0
357850	30	1	3	3.0	0.29	295.7	3.0																										.
366857	5	0	1	1.8	0.25	403.0	14.0																										.
366857	5	0	2	1.8	0.25	175.0	8.4	0	0	0	0.02	0.1	0.07	0.8	2.62	10.9	32.5	26.7	7.15	4.68	2.69	1.46	2.69	3.41	1.36	0.93	0.66	0.46	0.33	0.23	0.16	0.12	0
366857	5	0	3	1.8	0.25	217.0	9.8																										.
366857	10	0	1	2.3	0.26	397.1	14.8	0	0	0	0.08	0.39	0.28	5.27	4.67	5.43	3.43	5.49	6.95	11.4	10.8	10	6.98	7.75	5.32	5.13	3.92	2.93	2.16	1.17	0.26	0.18	0
366857	10	0	2	2.3	0.26	414.9	29.6	0	0	0	0	0	0	0.43	0.53	0.62	0.95	3.27	4.55	12.5	14.7	13	11.4	13.1	6.76	6.2	4.34	3.38	2.52	1.3	0.29	0.19	0
366857	10	0	3	2.3	0.26	621.2	18.0																										.
366857	15	0	1	2.8	0.47																												.
366857	15	0	2	2.8	0.47																												.
366857	15	0	3	2.8	0.47																												.
366857	5	1	1	1.5	0.17																												.
366857	5	1	2	1.5	0.17																												.
366857	5	1	3	1.5	0.17																												.
366857	10	1	1	1.6	0.22	376.9	6.6																										.
366857	10	1	2	1.6	0.22	369.6	7.6																										.
366857	10	1	3	1.6	0.22	328.1	9.5	0	0	0	0.01	0.04	0.03	1.89	9.03	28.4	21.3	10.3	5.69	3.05	2.3	2.92	2.58	3.77	2.35	1.91	1.57	1.27	0.92	0.5	0.11	0.07	0
366857	15	1	1	1.9	0.24	199.0	18.1																										.
366857	15	1	2	1.9	0.24	276.0	22.7	0	0	0	0.03	0.13	0.1	3.41	12.4	25.5	11.7	6.8	5.46	5.64	4.23	4.74	4.43	5.16	3.03	2.43	1.83	1.4	0.94	0.46	0.09	0.06	0
366857	15	1	3	1.9	0.24	210.0	15.5																										.
366857	20	1	1	2.1	0.18	373.8	19.9																										.

Appendix B

Mare coord	Dist. (m)	Shore	Quad	Depth (m)	velocity (m3/s)	Exch. P (ug/g)	Exch. N (ug/g)	phi -2	phi -1.5	phi -1	phi -0.5	phi 0	phi 0.5	phi 1	phi 1.5	phi 2	phi 2.5	phi 3	phi 3.5	phi 4	phi 4.5	phi 5	phi 5.5	phi 6	phi 6.5	phi 7	phi 7.5	phi 8	phi 8.5	phi 9	phi 9.5	phi 10	phi 10.5
366857	20	1	2	2.1	0.17	539.1	16.5	0	0	0	0.04	0.21	0.16	5.11	18	33	11	5.67	5.26	3.24	2.3	2.74	2.33	3.35	2.14	1.65	1.38	1.07	0.75	0.39	0.08	0.05	0
366857	20	1	3	2.1	0.17	479.8	14.1	0	0	0	0.02	0.1	0.08	4.12	19.9	37.8	11.6	4.35	4.56	2.15	1.91	2.45	1.44	2.52	2.09	1.48	1.27	0.96	0.67	0.36	0.07	0.05	0
366857	25	1	1	2.5	0.17	316.0	30.2																										.
366857	25	1	2	2.5	0.17	230.0	16.7	0	0	0	0.02	0.08	0.06	4.83	21.4	37.2	10.6	6.03	6.23	1.48	1.98	2.01	0.76	1.76	1.7	1.12	0.98	0.77	0.56	0.31	0.07	0.05	0
366857	25	1	3	2.5	0.17	259.0	24.3																										.
366857	30	1	1	3.0	0.48	359.1	2.9																										.
366857	30	1	2	3.0	0.48	247.4	1.9																										.
366857	30	1	3	3.0	0.48	256.3	1.7																										.
366857	35	1	1	3.0	0.49																												.
366857	35	1	2	3.0	0.49																												.
366857	35	1	3	3.0	0.49																												.
382855	5	0	1	1.0	0.08	358.0	19.7																										.
382855	5	0	2	1.0	0.08	310.0	19.8																										.
382855	5	0	3	1.0	0.08	317.0	19.0																										.
382855	15	0	1	1.0	0.37	229.0	5.8																										.
382855	15	0	2	1.0	0.37	384.0	5.1																										.
382855	15	0	3	1.0	0.37	216.0	1.2																										.
382855	25	0	1	1.3	0.63																												.
382855	25	0	2	1.3	0.63																												.
382855	25	0	3	1.3	0.63																												.
382855	10	1	1	0.3	0.00	433.8	11.1																										.
382855	10	1	2	0.3	0.00	562.7	22.1	0	0	0	0.14	0.65	0.48	0.69	0.54	2.34	4.51	15.2	13.9	10.3	8.54	7.97	6.37	9.34	6.03	4.3	3.06	2.42	1.7	0.83	0.17	0.11	0
382855	10	1	3	0.3	0.00	413.1	30.8	0	0	0	0.23	1.04	0.75	2.1	1.1	2.55	3.52	11.7	11.3	10.2	9.05	8.73	6.94	9.6	6.12	5.08	3.67	2.87	2.03	1.04	0.22	0.15	0
382855	20	1	1	0.8	0.14	233.3	4.8	0	0	0	1.64	7.59	5.99	12.5	10.5	12.4	12.5	10.5	8.76	4.3	2.55	2.18	1.53	2.95	1.35	0.93	0.65	0.46	0.33	0.23	0.16	0.12	0
382855	20	1	2	0.8	0.14	326.0	8.5																										.
382855	20	1	3	0.8	0.14	591.6	33.4	0	0	0	0.01	0.03	0.02	0.96	1.65	4.8	4.71	9.08	8.45	9.68	9.41	8.79	7.81	9.61	5.87	6.47	4.72	3.64	2.5	1.32	0.29	0.2	0
382855	30	1	1	1.0	0.21	199.6	37.8																										.
382855	30	1	2	1.0	0.21	181.4	10.4																										.
382855	30	1	3	1.0	0.21	183.8	9.7																										.
382855	40	1	1	0.8	0.52	157.4	5.2																										.
382855	40	1	2	0.8	0.52	207.0	8.1	0	0	0	1.98	9.15	7.42	16.4	12.1	11.8	12.1	10.1	7.46	3.51	1.41	1.04	0.76	1.82	0.97	0.67	0.47	0.33	0.24	0.17	0.12	0.08	0

Appendix B

Mstr coord	Dist. (m)	Shore	Quad	Depth (m)	velocity (m3/s)	Exch. P (ug/g)	Exch. N (ug/g)	phi -2	phi -1.5	phi -1	phi -0.5	phi 0	phi 0.5	phi 1	phi 1.5	phi 2	phi 2.5	phi 3	phi 3.5	phi 4	phi 4.5	phi 5	phi 5.5	phi 6	phi 6.5	phi 7	phi 7.5	phi 8	phi 8.5	phi 9	phi 9.5	phi 10	phi 10.5
382855	40	1	3	0.8	0.52	141.9	9.0																										.
576806	5	0	1	0.9	0.13	375.0	24.1																										.
576806	5	0	2	0.9	0.13	463.0	23.6																										.
576806	5	0	3	0.9	0.13	416.0	22.7																										.
576806	10	0	1	2.8	0.28	559.1	11.1	0	0	0	0.04	0.19	0.14	1.74	3.33	7.27	14	20.7	20.3	12.7	5.48	3.16	2.35	3.78	1.56	1.06	0.75	0.53	0.38	0.27	0.19	0.13	0
576806	10	0	2	2.8	0.28	310.8	4.4																										.
576806	10	0	3	2.8	0.28	403.7	0.7	0	0	0	0.09	0.41	0.29	10.9	22.5	31.1	20.1	8.53	3.21	0.72	0.49	0.2	0.08	0.33	0.32	0.23	0.16	0.11	0.08	0.06	0.04	0.03	0
576806	15	0	1	4.1	0.44	120.0	3.5	0	0	0	3.93	18.2	17.9	39.8	15.3	2.92	1.34	0.12	0.28	0.03	0	0	0	0.02	0.04	0.03	0.02	0.01	0.01	0.01	0.01	0	0
576806	15	0	2	4.1	0.44	124.0	5.1																										.
576806	15	0	3	4.1	0.44	107.0	5.4	0	0	0	3.72	17.2	16.5	41.2	15.8	3.04	1.59	0.14	0.36	0.07	0.03	0.04	0.03	0.09	0.09	0.07	0.05	0.03	0.02	0.02	0.01	0.01	0
576806	5	1	1	1.2	0.06																												.
576806	5	1	2	1.2	0.06																												.
576806	5	1	3	1.2	0.06																												.
576806	10	1	1	1.4	0.07	594.6	31.1	0	0	0	0	0.01	0.01	7.61	8.88	10	4.08	4.49	5.29	7.2	7.77	9.2	7.33	7.51	6.63	4.81	3.39	2.66	1.87	0.93	0.2	0.13	0
576806	10	1	2	1.4	0.07	552.8	20.2	0	0	0	0.01	0.03	0.02	10.5	12	9.97	3.07	4.24	4.39	6.43	7.23	8.34	7	7.4	6.21	4.55	3.22	2.5	1.74	0.86	0.18	0.12	0
576806	10	1	3	1.4	0.07	492.5	12.9	0	0	0	0	0	0	0	0	0	1.81	8.36	5.91	15	12.3	11.3	11	9.87	7.79	5.92	4.2	3.2	2.09	0.92	0.17	0.11	0
576806	15	1	1	1.5	0.10																												.
576806	15	1	2	1.5	0.10																												.
576806	15	1	3	1.5	0.10																												.
576806	20	1	1	1.7	0.06	754.6	46.0	0	0	0	0.03	0.14	0.1	10.9	13.7	13.5	4.71	5.39	6.1	5.96	6.41	7.02	5.03	7.01	4.34	3.48	2.35	1.8	1.26	0.59	0.11	0.08	0
576806	20	1	2	1.7	0.06	806.2	51.8	0	0	0	0	0	0	0	0	0	0.37	1.71	1.21	9.36	10.6	12.4	14	14.5	11.2	8.67	6.08	4.57	3.07	1.64	0.38	0.25	0
576806	20	1	3	1.7	0.06	918.5	65.0	0	0	0	0	0	0	1.17	2.57	2.61	0.87	2.23	4.01	9.44	11.1	13.9	11.7	11.1	9.26	6.72	4.62	3.4	2.38	1.44	0.71	0.82	0.01
576806	25	1	1	2.0	0.14																												.
576806	25	1	2	2.0	0.14																												.
576806	25	1	3	2.0	0.14																												.
576806	30	1	1	2.3	0.07	946.9	61.2	0	0	0	0	0	0	0	0	0	0.29	1.35	0.95	10.3	11.4	13.2	14.4	14.2	10.8	8.2	5.62	4.28	3.01	1.58	0.35	0.23	0
576806	30	1	2	2.3	0.07	1010.9	55.8	0	0	0	0	0	0	0	0	0	0.21	0.98	0.69	10	11.3	12.7	14	14.1	10.8	8.59	6.1	4.75	3.35	1.75	0.38	0.26	0
576806	30	1	3	2.3	0.07	1022.1	73.8	0	0	0	0	0	0	0	0	0	0.25	1.55	3.33	9.41	11.3	14.4	12.5	12.3	10.7	8.37	5.9	4.59	3.19	1.64	0.35	0.24	0
576806	35	1	1	2.3	0.06	680.0	50.0																										.
576806	35	1	2	2.3	0.06	767.0	45.2	0	0	0	0	0	0	0.19	0.9	0.83	0.6	1.59	2.76	7.63	10.4	15.3	12.8	13.1	11	7.77	5.89	4.41	2.98	1.49	0.3	0.2	0
576806	35	1	3	2.3	0.06	515.0	28.2	0	0	0	0	0	0	6.53	6.88	5.69	1.67	1.95	2.93	6.32	8.37	11.7	9.93	11	8.56	6.32	4.7	3.54	2.35	1.21	0.26	0.17	0

Appendix B

Merc coord	Dist. (m)	Shore	Quad	Depth (m)	velocity (m3/s)	Exch. P (ug/g)	Exch. N (ug/g)	phi -2	phi -1.5	phi -1	phi -0.5	phi 0	phi 0.5	phi 1	phi 1.5	phi 2	phi 2.5	phi 3	phi 3.5	phi 4	phi 4.5	phi 5	phi 5.5	phi 6	phi 6.5	phi 7	phi 7.5	phi 8	phi 8.5	phi 9	phi 9.5	phi 10	phi 10.5
576806	40	1	1	2.7	0.11	732.8	65.5	0	0	0	0	0	0	0	0	0	0.12	0.8	2.52	8.33	10.9	14.9	12.5	14	10.6	8.44	6.32	4.73	3.43	1.76	0.37	0.24	0
576806	40	1	2	2.7	0.11	800.5	58.1	0	0	0	0	0	0	0	0.03	0.05	0.54	1.35	2.84	8.87	11.6	16	12.7	12.2	10.7	7.74	5.83	4.35	3.13	1.56	0.32	0.21	0
576806	40	1	3	2.7	0.11	790.1	70.9	0	0	0	0	0	0	0	0	0	0.45	2.08	1.47	8.84	9.61	11.2	13.6	14.8	11.4	8.76	6.54	5.06	3.52	1.92	0.45	0.3	0.01
576806	45	1	1	2.6	0.06	777.0	55.9	0	0	0	0	0	0	0	0	0	0.41	1.91	1.35	13	12.5	13	13.6	12.6	9.72	7.51	5.27	4.19	2.96	1.53	0.33	0.22	0
576806	45	1	2	2.6	0.06	563.0	39.2																										.
576806	45	1	3	2.6	0.06	781.0	58.5																										.
576806	50	1	1	2.6	0.03	593.0	25.2	0	0	0	0	0	0	8.38	7.74	3.92	0.37	1.12	2.82	8.36	9.48	11.9	10.5	9.22	8.14	5.99	4.16	3.1	2.17	1.3	0.64	0.73	0.01
576806	50	1	2	2.6	0.03	653.7	38.5	0	0	0	0	0	0	3.6	5.8	3.75	0.47	1.7	3.12	8.62	9.75	12.5	10.6	11	8.95	6.63	4.65	3.47	2.46	1.47	0.71	0.8	0.01
576806	50	1	3	2.6	0.03	742.5	28.9																										.
576806	55	1	1	2.4	0.04	579.0	43.5																										.
576806	55	1	2	2.4	0.04	541.0	33.0																										.
576806	55	1	3	2.4	0.04	598.0	62.9																										.
576806	60	1	1	2.5	0.05	929.7	87.8	0	0	0	0	0	0	0	0	0	0.16	1.11	2.77	8.49	10.7	15	11.7	13.7	11.1	8.58	6.08	4.79	3.37	1.74	0.38	0.25	0
576806	60	1	2	2.5	0.05	1055.5	186.6	0	0	0	0	0	0	0	0	0	0.2	1.2	2.66	7.35	9.92	15.9	12.4	12.6	11.9	8.54	6.45	4.97	3.38	1.81	0.4	0.27	0
576806	60	1	3	2.5	0.05	862.0	67.8	0	0	0	0	0	0	0	0	0	0.24	1.48	3.4	8.02	10.2	15.7	11.1	12	11.6	8.28	6.57	5.08	3.57	1.98	0.45	0.3	0.01
576806	65	1	1	2.8	0.11	896.0	61.3																										.
576806	65	1	2	2.8	0.11	888.0	80.2	0	0	0	0	0	0	0	0	0	0.19	1.68	3.62	8.72	10.5	14.4	11	9.97	12.6	9.36	6.7	5.22	3.72	1.82	0.35	0.23	0
576806	65	1	3	2.8	0.11	874.0	70.0	0	0	0	0	0	0	0	0	0	0.28	1.64	3.5	8.99	11	14	10.6	13.2	11	8.67	6.32	4.96	3.43	1.77	0.39	0.26	0
576806	70	1	1	3.3	0.28	396.9	20.8																										.
576806	70	1	2	3.3	0.28	348.2	1.8																										.
576806	70	1	3	3.3	0.28	356.2	10.4	0	0	0	0.99	4.55	3.51	26.3	16.6	10.3	3.7	4.34	3.31	2.76	3.27	3.4	3.22	4.6	2.63	2.13	1.61	1.28	0.9	0.44	0.09	0.06	0
576806	75	1	1	3.5	0.35	256.0	2.7																										.
576806	75	1	2	3.5	0.35	300.0	6.2	0	0	0	0.65	3	2.2	19.6	20.9	21.7	16.1	8.38	2.41	1.18	0.78	0.42	0.42	0.81	0.46	0.32	0.22	0.16	0.11	0.08	0.06	0.04	0
576806	75	1	3	3.5	0.35	184.0	2.2	0	0	0	1.58	7.3	5.72	37.4	25.4	15	5	1.73	0.47	0.07	0.06	0.04	0.03	0.07	0.05	0.04	0.03	0.02	0.01	0.01	0.01	0	0
576806	80	1	1	3.5	0.46	190.1	3.0	0	0	0	1.91	8.84	7.11	37	25	14.2	4.16	0.83	0.4	0.06	0.04	0.04	0.03	0.09	0.08	0.05	0.04	0.03	0.02	0.01	0.01	0.01	0
576806	80	1	2	3.5	0.46	270.4	2.0																										.
576806	80	1	3	3.5	0.46	248.0	3.4																										.
601819	5	0	1	0.6	0.13																												.
601819	5	0	2	0.6	0.13																												.
601819	5	0	3	0.6	0.13																												.
601819	10	0	1	1.1	0.25	584.3	3.2																										.

Appendix B

Merc coord	Dist. (m)	Shore	Quad	Depth (m)	velocity (m3/s)	Exch. P (ug/g)	Exch. N (ug/g)	phi -2	phi -1.5	phi -1	phi -0.5	phi 0	phi 0.5	phi 1	phi 1.5	phi 2	phi 2.5	phi 3	phi 3.5	phi 4	phi 4.5	phi 5	phi 5.5	phi 6	phi 6.5	phi 7	phi 7.5	phi 8	phi 8.5	phi 9	phi 9.5	phi 10	phi 10.5
601819	10	0	2	1.1	0.25	535.5	4.7																										.
601819	10	0	3	1.1	0.25	540.2	2.9																										.
601819	15	0	1	2.2	0.54	437.0	25.6																										.
601819	15	0	2	2.2	0.54	299.0	7.9																										.
601819	15	0	3	2.2	0.54																												.
601819	20	0	1	2.5	0.69	0.0	0.0																										.
601819	20	0	2	2.5	0.69	0.0	0.0																										.
601819	20	0	3	2.5	0.69	0.0	0.0																										.
601819	5	1	1	1.2	0.02	144.0	4.6																										.
601819	5	1	2	1.2	0.02																												.
601819	5	1	3	1.2	0.02	426.0	6.4																										.
601819	10	1	1	2.2	0.58	0.0	0.0																										.
601819	10	1	2	2.2	0.58	0.0	0.0																										.
601819	10	1	3	2.2	0.58	0.0	0.0																										.
846788	5	0	1	1.2	0.62																												.
846788	5	0	2	1.2	0.62																												.
846788	5	0	3	1.2	0.62																												.
846788	10	1	1	0.9	0.60																												.
846788	10	1	2	0.9	0.60																												.
846788	10	1	3	0.9	0.60																												.
846788	15	1	1	1.2	0.62	0.0	0.0																										.
846788	15	1	2	1.2	0.62	0.0	0.0																										.
846788	15	1	3	1.2	0.62	0.0	0.0																										.
973912	5	0	1	0.8	0.16	169.0	4.4	0	0	0	1.51	6.96	5.42	17.7	15.1	15.9	16.2	10.8	4.18	2.7	0.86	0.42	0.3	0.5	0.25	0.17	0.12	0.09	0.06	0.04	0.03	0.02	0
973912	5	0	2	0.8	0.16	195.0	4.5	0	0	0	0.74	3.4	2.59	17.6	12.9	9.43	4.11	8.85	6.8	5.23	5.39	4.99	4.22	5.27	2.85	2.25	1.47	1.01	0.62	0.26	0.04	0.03	0
973912	5	0	3	0.8	0.16	392.0	5.4																										.
973912	10	0	1	1.1	0.13	473.9	11.5																										.
973912	10	0	2	1.1	0.13	401.5	15.6																										.
973912	10	0	3	1.1	0.13	329.7	8.3	0	0	0	0.05	0.22	0.17	4.31	8.78	13.1	6.5	12.1	10.9	9.11	7.61	6.46	4.23	5.75	3.64	2.75	1.76	1.3	0.88	0.36	0.06	0.04	0
973912	15	0	1	1.3	0.24	321.0	17.8																										.
973912	15	0	2	1.3	0.24	467.0	20.5	0	0	0	0	0	0	0.01	0.32	3.96	5.89	10.4	8.38	9.58	10.2	11.4	8.93	11.4	6.59	5.3	3.32	2.23	1.37	0.58	0.1	0.07	0

Appendix B

Merc coord	Dist. (m)	Shore	Quad	Depth (m)	velocity (m3/s)	Exch. P (ug/g)	Exch. N (ug/g)	phi -2	phi -1.5	phi -1	phi -0.5	phi 0	phi 0.5	phi 1	phi 1.5	phi 2	phi 2.5	phi 3	phi 3.5	phi 4	phi 4.5	phi 5	phi 5.5	phi 6	phi 6.5	phi 7	phi 7.5	phi 8	phi 8.5	phi 9	phi 9.5	phi 10	phi 10.5
973912	15	0	3	1.3	0.24	221.0	13.8																										.
973912	20	0	1	1.3	0.16	221.0	8.6	0	0	0	0.02	0.07	0.05	1.3	5.49	20.1	34.1	14.8	4.09	4.38	2.57	2.51	2.62	3.63	1.4	0.95	0.67	0.47	0.34	0.24	0.17	0.12	0
973912	20	0	2	1.3	0.16	244.0	8.6																										.
973912	20	0	3	1.3	0.16	223.1	10.0																										.
973912	25	0	1	1.3	0.13	352.0	14.7	0	0	0	0.64	2.96	2.18	10.7	16.7	28.2	26.6	9	1.99	0.48	0.07	0.06	0.04	0.1	0.08	0.06	0.04	0.03	0.02	0.01	0.01	0.01	0
973912	25	0	2	1.3	0.13	12.5	15.2	0	0	0	1.29	5.97	4.58	22.2	23.7	24	13.3	3.53	0.8	0.24	0.06	0.04	0.03	0.08	0.06	0.05	0.03	0.02	0.02	0.01	0.01	0.01	0
973912	25	0	3	1.3	0.13	410.0	22.5	0	0	0	1.41	6.53	5.05	21.6	22.9	23.6	13.2	3.3	0.94	0.38	0.16	0.13	0.13	0.23	0.14	0.1	0.07	0.05	0.03	0.02	0.02	0.01	0
973912	30	0	1	1.5	0.23	328.2	21.8																										.
973912	30	0	2	1.5	0.23	306.5	19.2	0	0	0	0.01	0.05	0.04	0.98	4.02	14.7	16.5	19.7	10.5	4.87	5.04	4.65	4.18	5.34	2.72	2.53	1.72	1.25	0.81	0.35	0.06	0.04	0
973912	30	0	3	1.5	0.23	353.3	18.2																										.
973912	35	0	1	2.0	0.51	203.0	5.5																										.
973912	35	0	2	2.0	0.51	202.0	5.0	0	0	0	0	0.01	0	0.58	3.46	15.2	13.9	16.9	10.9	6.33	5.13	4.19	3.27	5.19	3.36	3.12	2.7	2.36	1.85	1.09	0.27	0.18	0
973912	35	0	3	2.0	0.51	192.0	5.0																										.
973912	5	1	1	1.5	0.20	536.0	35.4	0	0	0	0	0	0	0	0	0	0.5	3.98	7.28	11.2	12.4	14.2	10.3	13.9	8.69	6.98	4.35	3.01	1.96	0.88	0.17	0.11	0
973912	5	1	2	1.5	0.20	578.0	46.5																										.
973912	5	1	3	1.5	0.20	22.5	41.9	0	0	0	0	0	0	0	0	0	0.39	2.36	4.24	11.3	11.9	15.3	14.6	10.7	11.2	7.39	4.47	3.08	1.94	0.88	0.18	0.12	0
973912	10	1	1	2.1	0.32	544.9	47.9	0	0	0	0	0	0	0	0.09	1.22	2.55	8.48	8.88	11.2	11.8	11.9	9.65	12.2	7	6.16	3.78	2.6	1.64	0.72	0.14	0.09	0
973912	10	1	2	1.1	0.32	468.2	25.7	0	0	0	0	0	0	0.01	0.06	1.23	3.38	11.3	10.7	11	10.9	10.9	8.91	11.7	6.66	5.27	3.32	2.31	1.46	0.64	0.12	0.08	0
973912	10	1	3	1.1	0.32	549.7	44.7	0	0	0	0	0	0	0.01	0.06	0.81	2.22	8.22	9	11.4	11.8	12.2	9.87	12.6	7.25	5.94	3.64	2.52	1.53	0.68	0.14	0.09	0
973912	15	1	1	2.0	0.33	212.0	8.3																										.
973912	15	1	2	2.0	0.33	262.0	8.4																										.
973912	15	1	3	2.0	0.33	436.0	32.4																										.
973912	20	1	1	1.8	0.48	105.1	2.2	0	0	0	1.35	6.21	4.79	20.8	15.2	12.6	10.1	9.22	5.8	3.51	2.48	1.81	1.27	20.9	0.9	0.61	0.43	0.31	0.22	0.15	0.11	0.08	0
973912	20	1	2	1.8	0.48	149.8	4.3																										.
973912	20	1	3	1.8	0.48																												.
984905	5	0	1	2.0	0.59	395.0	20.4																										.
984905	5	0	2	2.0	0.59	280.0	14.2																										.
984905	5	0	3	2.0	0.59	286.0	10.5																										.
984905	10	0	1	2.5	0.67	0.0	0.0																										.
984905	10	0	2	2.5	0.67	0.0	0.0																										.
984905	10	0	3	2.5	0.67	0.0	0.0																										.

Appendix B

Merc coord	Dist. (m)	Shore	Quad	Depth (m)	velocity (m3/s)	Exch. P (ug/g)	Exch. N (ug/g)	phi -2	phi -1.5	phi -1	phi -0.5	phi 0	phi 0.5	phi 1	phi 1.5	phi 2	phi 2.5	phi 3	phi 3.5	phi 4	phi 4.5	phi 5	phi 5.5	phi 6	phi 6.5	phi 7	phi 7.5	phi 8	phi 8.5	phi 9	phi 9.5	phi 10	phi 10.5
984905	15	0	1	2.6	0.77	0.0	0.0																										.
984905	15	0	2	2.6	0.77	0.0	0.0																										.
984905	15	0	3	2.6	0.77	0.0	0.0																										.
984905	5	1	1	0.3	0.22	158.0	2.9	0	0	0	0.03	0.13	0.09	1.53	5.56	19.2	41.6	24.2	4.21	1.42	0.42	0.22	0.28	0.42	0.21	0.15	0.1	0.07	0.05	0.04	0.03	0.02	0
984905	5	1	2	0.3	0.22	206.0	3.0																										.
984905	5	1	3	0.3	0.22	235.0	7.8																										.
984905	10	1	1	0.5	0.22	172.6	4.4																										.
984905	10	1	2	0.5	0.22	206.9	4.4																										.
984905	10	1	3	0.5	0.22	250.6	8.3																										.
984905	15	1	1	0.5	0.13	221.0	8.6	0	0	0	0.01	0.06	0.04	1.24	3.92	12.7	25.7	18	7.54	6.09	5.32	4.88	4.21	5.06	1.73	1.17	0.82	0.58	0.41	0.29	0.21	0.15	0
984905	15	1	2	0.5	0.13	313.0	14.1																										.
984905	15	1	3	0.5	0.13	277.0	13.0																										.
984905	20	1	1	0.3	0.21	231.0	10.8	0	0	0	0.01	0.03	0.02	0.86	3.6	14.4	35.7	23.4	6.42	4.53	1.94	1.6	1.98	2.53	0.94	0.63	0.45	0.32	0.22	0.16	0.11	0.08	0
984905	20	1	2	0.3	0.21	222.6	5.6																										.
984905	20	1	3	0.3	0.21	300.3	11.4	0	0	0	0.01	0.05	0.04	1.01	3.37	12.8	17.3	23.1	12.7	5.07	4.98	4.05	3.4	4.54	2.22	1.94	1.4	1.04	0.67	0.31	0.06	0.04	0
984905	25	1	1	0.5	0.19	326.0	16.8	0	0	0	0.01	0.04	0.03	0.68	2.63	10.4	29	26.4	8.62	5.14	3.86	2.69	2.85	3.68	1.29	0.87	0.62	0.44	0.31	0.22	0.15	0.11	0
984905	25	1	2	0.5	0.19	338.0	11.3	0	0	0	0	0.02	0.01	0.55	2.52	11	31.7	26.1	7.28	5.2	3.52	2.4	2.93	3.4	1.08	0.73	0.51	0.36	0.26	0.18	0.13	0.09	0
984905	25	1	3	0.5	0.19	349.0	8.8	0	0	0	0.01	0.05	0.03	0.73	2.79	11.7	33.9	27.2	7.9	4.68	2.55	1.67	2.04	2.34	0.78	0.52	0.37	0.26	0.19	0.13	0.09	0.07	0
984905	30	1	1	0.7	0.41	200.8	2.3																										.
984905	30	1	2	0.7	0.41	188.1	2.1																										.
984905	30	1	3	0.7	0.41	174.5	2.1	0	0	0	0.27	1.25	0.9	14.3	26.3	34.3	19.2	2.38	0.51	0.31	0.02	0.03	0.02	0.05	0.05	0.04	0.03	0.02	0.01	0.01	0.01	0	0